Spinneret Morphology and the Phylogeny of Haplogyne Spiders (Araneae, Araneomorphae)

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ABSTRACT

Scanning electron microscopy is used to survey the spinneret morphology of representatives of 47 genera of araneomorph spiders with haplogyne female genitalia. In most of the examined "lower" araneomorphs—some 20 families of hypochiloids, austrochiloids, and classical Haplogynae (including the cribellate family Filistatidae)—there is no evidence of cylindrical gland spigots. Only in the Leptonetidae and Telemidae do females have a type of spigot, on both the posterior median and posterior lateral spinnerets, that is not also present in males, and that may therefore serve cylindrical glands. Cylindrical glands seem otherwise to be synapomorphic for a large group of about 70 "higher" araneomorph families corresponding roughly to the classical concept of Entelegynae (but including those palpimanoid and orbicularian taxa with haplogyne females). A data matrix including 67 characters for 35 haplogyne and eight related genera, belonging to 36 families, is presented and analyzed. The results suggest that the classical Haplogynae form a monophyletic group but that the superfamily Scytodoidea is paraphyletic. Paracribellar spigots, previously reported only on the posterior median spinnerets, apparently occur also on the posterior lateral spinnerets of austrochilids and filistatids. The family Loxoscelidae is placed as a junior synonym of Sicariidae.

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INTRODUCTION

This paper had its origin as an attempt to answer a single question: where in the phylogeny of araneomorph spiders did cylindrical silk glands, and their associated spigots, first appear? That question initially arose in the course of examining spinneret morphology in hunting spiders of the family Clubionidae and their allies. One of the major differences detected was the presence (in at least some phrurolithine, liocranine, corinnine, castianeirine, and tracheline genera) or absence (in at least some clubionine, anyphaenid, and miturgid genera) of a spigot type thought to serve the cylindrical glands. As cylindrical gland spigots are found in all the gnaphosoid taxa examined to date (Platnick, 1990) and in most other entelegyne families (Kovoor, 1987; Coddington, 1990b), their loss might unite some taxa currently placed in the Clubionidae, Anyphaenidae, and Miturgidae.

Kovoor (1987) noted from her histological studies that cylindrical glands are absent in seven families of araneomorphs: the Filistatidae, Scytodidae, Pholcidae, Dysderidae, Segestriidae, Clubionidae, and Salticidae. Because the first five of those families are haplogyne taxa thought to represent some of the most plesiomorphic groups of araneomorphs, whereas the Clubionidae and Salticidae are entelegyne hunting spiders, this distribution suggested that cylindrical glands might characterize a large group of "higher" araneomorphs, despite their possible loss in some entelegyne spider lineages.

Answering this question by direct histological examination would obviously be highly desirable, but is unlikely to be accomplished in the near future because of the difficulty of obtaining adequately fixed specimens of most of the less common, and geographically more restricted, families. This paper therefore attempts instead to suggest a preliminary answer through the use of scanning electron microscopy. Because cylindrical glands are used in egg case construction, occur in adult (and occasionally juvenile; see Yu and Coddington, 1990) females but not in males, and open on both the posterior median and posterior lateral spinnerets (Ko-

voor, 1977a, 1987; Coddington, 1989), the occurrence of a spigot type, on those spinneret pairs, that is present in females but not in males can suggest that cylindrical glands are present. Unfortunately, such a distribution of spigot types is a necessary but not a sufficient condition for concluding that cylindrical glands are present, as males may have lost their aciniform and/or minor ampullate glands. Thus, spigot morphology can most reliably suggest that cylindrical glands are present in those species where the posterior median spinnerets bear three spigot types in females but only two in males.

Scanning electron micrographs are presented here of the anterior lateral (ALS), posterior median (PMS), and posterior lateral spinnerets (PLS) of representatives of 47 genera of araneomorphs whose females have haplogyne genitalia, belonging to 27 families. Twenty-three of those families are exclusively haplogyne in genitalic morphology, but four (Micropholcommatidae, Anapidae, Uloboridae, and Tetragnathidae) also contain entelegyne genera. Where possible, we have tried to present scans of adult males as well as females for at least one representative of each relevant family. The micrographs generally have the spinnerets positioned with their anterior edge at the top of the image; because they have been variably reduced for publication, the magnification figures supplied in the legends provide only relative scale information. The distinction made below between major and minor ampullate glands refers only to whether those glands serve spigots on the ALS, or on the PMS and/or PLS, respectively. The specimens used are deposited in the collections of the American Museum of Natural History, the National Museum of Natural History, and the Otago Museum.

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PHYLOGENETIC CONTEXT

Although we are very far from having a detailed hypothesis of the interrelationships of the 90 or more currently recognized families of araneomorph spiders, information accumulated over the last century has provided a rough estimate of some of the major lineages (Coddington, 1990b). Differences in genitalic and spinneret morphology have long been used to separate some clusters of families. Those araneomorphs in which the female genitalia remain haplogyne (as in liphistiids and mygalomorphs), and those araneomorphs which still retain a functional cribellum, are considered more primitive than those with entelegyne female genitalia (i.e., with separate copulatory and fertilization ducts) or those in which a functional cribellum has been transformed into a colulus (or lost completely). The presence of a colulus is clearly not synapomorphic for all the taxa possessing that structure; many species are known, for example, in which females are cribellate but males are colulate, and there are many monophyletic groups which include both cribellate and ecribellate members. Similarly, entelegyny is not unambiguously synapomorphic for all entelegyne taxa either, as the family Uloboridae, for example, contains both haplogyne and entelegyne members but appears nevertheless to be monophyletic (Opell, 1979; Coddington, 1990a). The superfamily Palpimanoidea also contains a mixture of entelegyne and haplogyne families; clearly, the distribution of haplogyny and entelegyny is homoplasious (Forster, 1980; Forster and Platnick, 1984). It is not clear, however, whether the homoplasy results only from secondary loss of either condition or from parallel gain in different clades. How many independent losses of the cribellum, and how many independent gains (and/or subsequent losses) of separate fertilization ducts, occurred during araneomorph phylogeny are questions that can only be answered when a full data matrix for all the relevant taxa can be assembled and analyzed.

Some suprafamilial groupings of araneo-

morphs have been supported by cladistic arguments, including the Hypochiloidea and Austrochiloidea (Forster et al., 1987), Dysderoidea (Forster and Platnick, 1985), Palpimanoidea (Forster and Platnick, 1984), Araneoidea, Orbiculariae, Entelegynae and subsidiary groups (Coddington, 1986, 1989, 1990b), and Gnaphosoidea (Platnick, 1990). Relatively few characters, however, have been suggested to unite larger groups; chief among them are grate- and canoe-shaped tapeta (Homann, 1971), a divided cribellum, and the presence of a retrolateral tibial apophysis on the male palp (Coddington, 1990a; Griswold, 1990; Sierwald, 1990).

The taxa investigated here include primarily species in which the female genitalia are haplogyne; of these, a functional cribellum is retained only in the Hypochilidae, Austrochilidae, some Gradungulidae, Filistatidae, and Uloboridae. The first four of these are basal araneomorph groups, but the uloborids have been convincingly (if not undisputedly) placed, along with the Deinopidae, as the closest relatives of the Araneoidea (Coddington, 1986, 1989). Many of the classical haplogyne families have been associated with the Filistatidae by the presence of a cheliceral lamina (Brignoli, 1978); this group (the superfamily Scytodoidea) includes the Filistatidae, Scytodidae, Sicariidae, Loxoscelidae, Drymusidae, Diguetidae, Plectreuridae, Pholcidae, Tetrablemmidae, Caponiidae, and Ochyroceratidae. If Scytodoidea (including the cribellate Filistatidae) is monophyletic, however, the other classical haplogyne families (namely the four dysderoid families plus the Leptonetidae and Telemidae) will require at least one additional loss of a functional cribellum on any cladogram.

If, as Kovoor's work implies, the presence of cylindrical gland spigots can be used as a synapomorphy for "higher" araneomorphs, we should expect to find them, among haplogynes, only in those taxa that are more closely related to entelegyne groups than to the classical "Haplogynae." In particular, (1) the haplogyne taxa associated with entelegynes in the Palpimanoidea and Orbiculariae should have cylindrical gland spigots, whereas (2) the more basal haplogyne families should not. As the results below indicate, the first prediction may be accurate, but the sec-

TABLE 1
Taxa Figured
(Taxa examined, their familial position, and the figure
numbers of their spinneret micrographs.)

Hypochilidae	
Hypochilus pococki Platnick	1–12
Ectatosticta davidi (Simon)	see Forster et al., 1987: figs. 31–36
Gradungulidae	
Gradungula sorenseni Forster	13–18
Pianoa isolata Forster	19–22
Macrogradungula moonya Gray	297–304
Austrochilidae	
Austrochilus melon Platnick	27–34
Thaida peculiaris Karsch	35–41
Hickmania troglodytes (Higgins and Petterd)	42–50
Filistatidae	
Kukulcania hibernalis (Hentz)	51–61
Filistata insidiatrix (Forskal)	62–72
Scytodidae	
Scytodes sp. (Texas)	73–76
Sicariidae	
Sicarius sp. (Chile)	77–82
Drymusidae	
Drymusa sp. (South Africa)	83–88
Loxoscelidae	
Loxosceles reclusa Gertsch and Mulaik	89–95
Loxosceles laeta (Nicolet)	96
Loxosceles rufescens (Dufour)	97–102
Diguetidae	
Diguetia spp.	103–111
Segestrioides tofo Platnick	112–117
Segestrioides bicolor Keyserling	118–120
Plectreuridae	
Plectreurys tristis Simon	121–126
Kibramoa suprenans Chamberlin	127–132
Pholcidae	
Pholcus phalangioides (Fuesslin)	133–138
Tetrablemmidae	
Caraimatta sbordonii (Brignoli)	139–144
Gen. sp. (Singapore)	23–26
Caponiidae	
Nops ovalis Banks	145–153
Ochyroceratidae	
Ochyrocera sp. (Colombia)	162–167
Dysderidae	
Dysdera crocota C. L. Koch	168–173

TABLE 1—(*Continued*)

|	
Segestriidae	
Segestria senoculata (Linnaeus)	174–179
Ariadna sp. (New Zealand)	154–158
Gippsicola sp. (New Zealand)	159–161
Oonopidae	
Dysderina plena O. P.-Cambridge	180–185
Xyphinus sp. (Singapore)	186–190
Gamasomorpha sp. (Singapore)	191–194
Orsolobidae	
Mallecolobus sanus Forster and Platnick	198–203
Wiltonia graminicola Forster and Platnick	204–208
Maoriata magna (Forster)	209–211
Subantarctia trina Forster and Platnick	212–215
Leptonetidae	
Appaleptoneta gertschi (Barrows)	216–221
Telemidae	
Usofila pacifica (Banks)	222–227
Archaeidae	
Archaea workmani (O. P.-Cambridge)	228–233
Mecysmaucheniidae	
Mecysmauchenius segmentatus Simon	234–239
Aotearoa magna (Forster)	195–197
Micropholcommatidae	
Tricellina gertschi (Forster and Platnick)	240–244
Huttoniidae	
Huttonia palpimanoides O. P.-Cambridge	246–248, 305–310
Palpimanidae	
Otiothops pentucus Chickering	245, 257–259
Uloboridae	
Waitkera waitakerensis (Chamberlain)	260–269
Tetragnathidae	
Tetragnatha versicolor Walckenaer	270–275, 282, 287–290
Pachygnatha autumnalis Keyserling	276–281, 283–286
Anapidae	
Crassanapis chilensis Platnick and Forster	291–296
Novanapis spinipes (Forster)	249–256

ond is only partly so, with the families Telemidae and Leptonetidae presenting potentially significant anomalies.

Table 1 provides a list of the taxa whose spinnerets are illustrated here, along with the figure numbers of the relevant micrographs. We present first a descriptive account of the spinneret morphology of these taxa; then we outline a data matrix, and provide a cladistic analysis, which attempt to resolve haplogyne familial interrelationships by the use of spinneret and other characters.
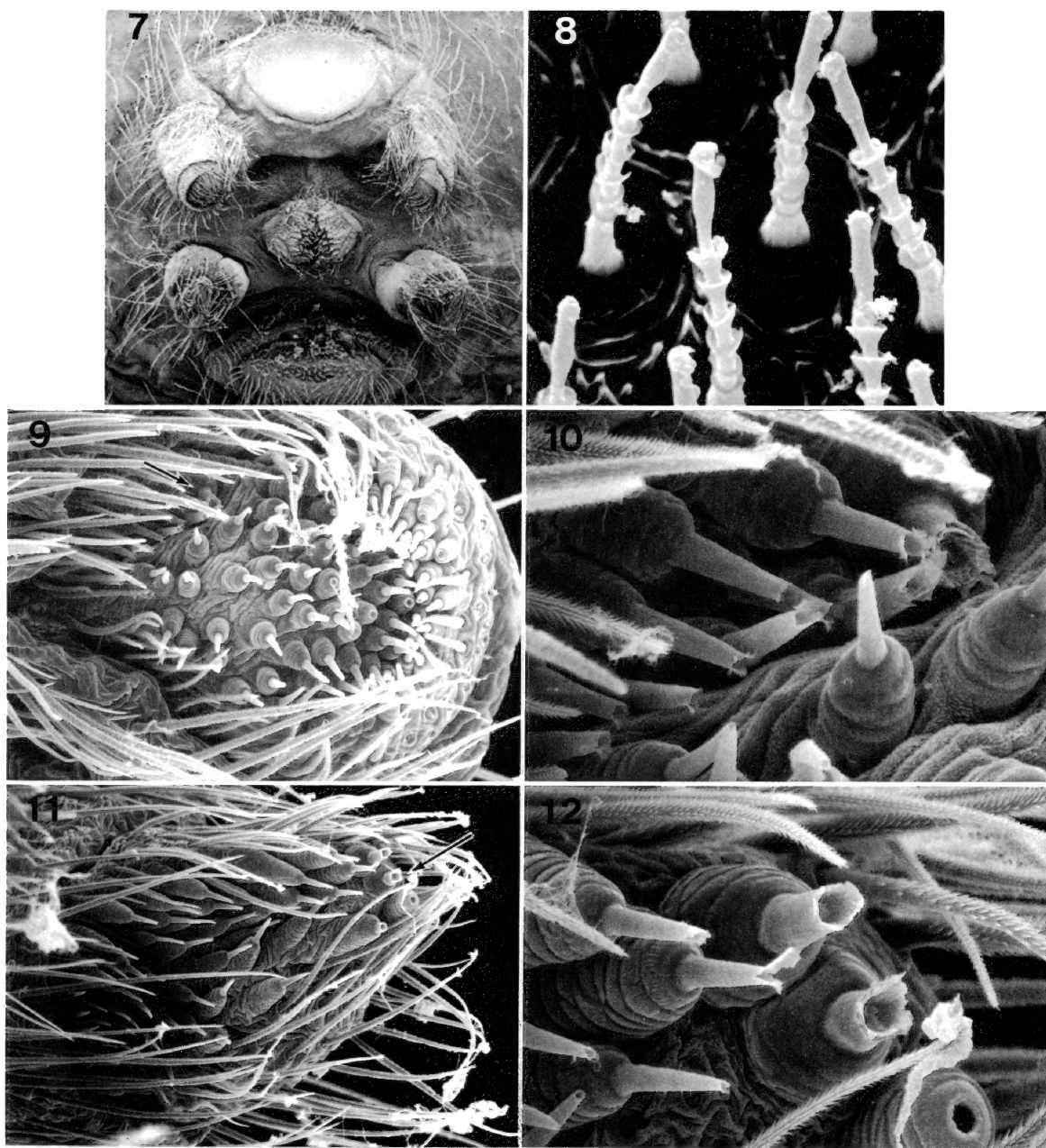
## HAPLOGYNE SPINNERET MORPHOLOGY
THE FAMILY HYPOCHILIDAE

The spinning apparatus of *Hypochilus gertschi* Hoffman was described in a posthumous paper by Glatz (1972: figs. 12–16), who iden-
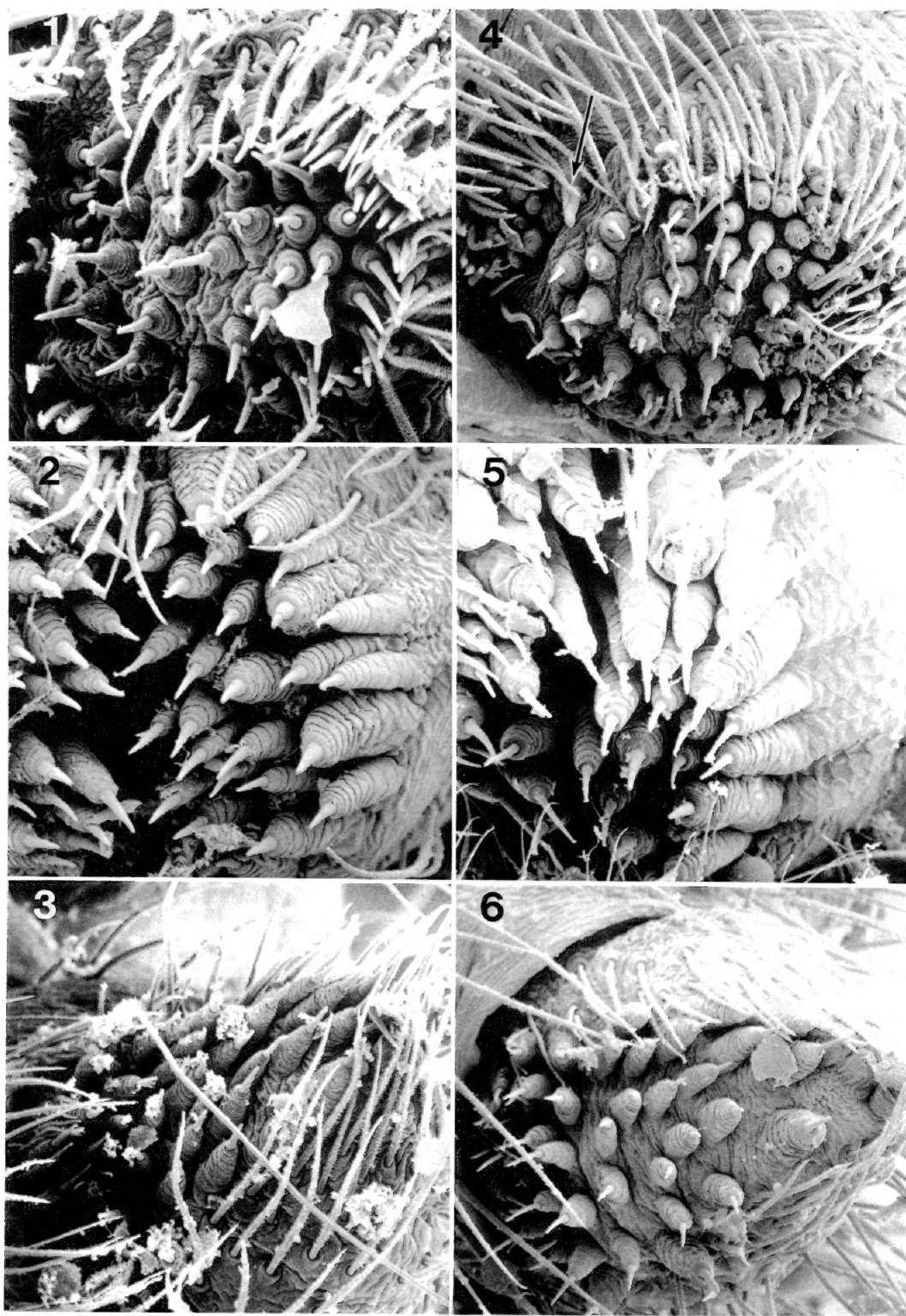
Figs. 1–6. *Hypochilus pococki* Platnick. 1–3. Female. 4–6. Male. **1, 4.** ALS, 580×, 445× (arrow to major ampullate gland spigot field). **2, 5.** PMS, 520×, 645×. **3, 6.** PLS, 380×, 395×.

Figs. 7–12. *Hypochilus pococki* Platnick, female. **7.** Spinning field, 55×. **8.** Cribellar spigots, 7015×. **9, 10.** ALS, 405× (arrow to major ampullate gland spigot field), and detail of those spigots, 1620×. **11, 12.** PLS, 300× (arrow to distal spigots with enlarged shafts), and detail of those spigots, 1350×.
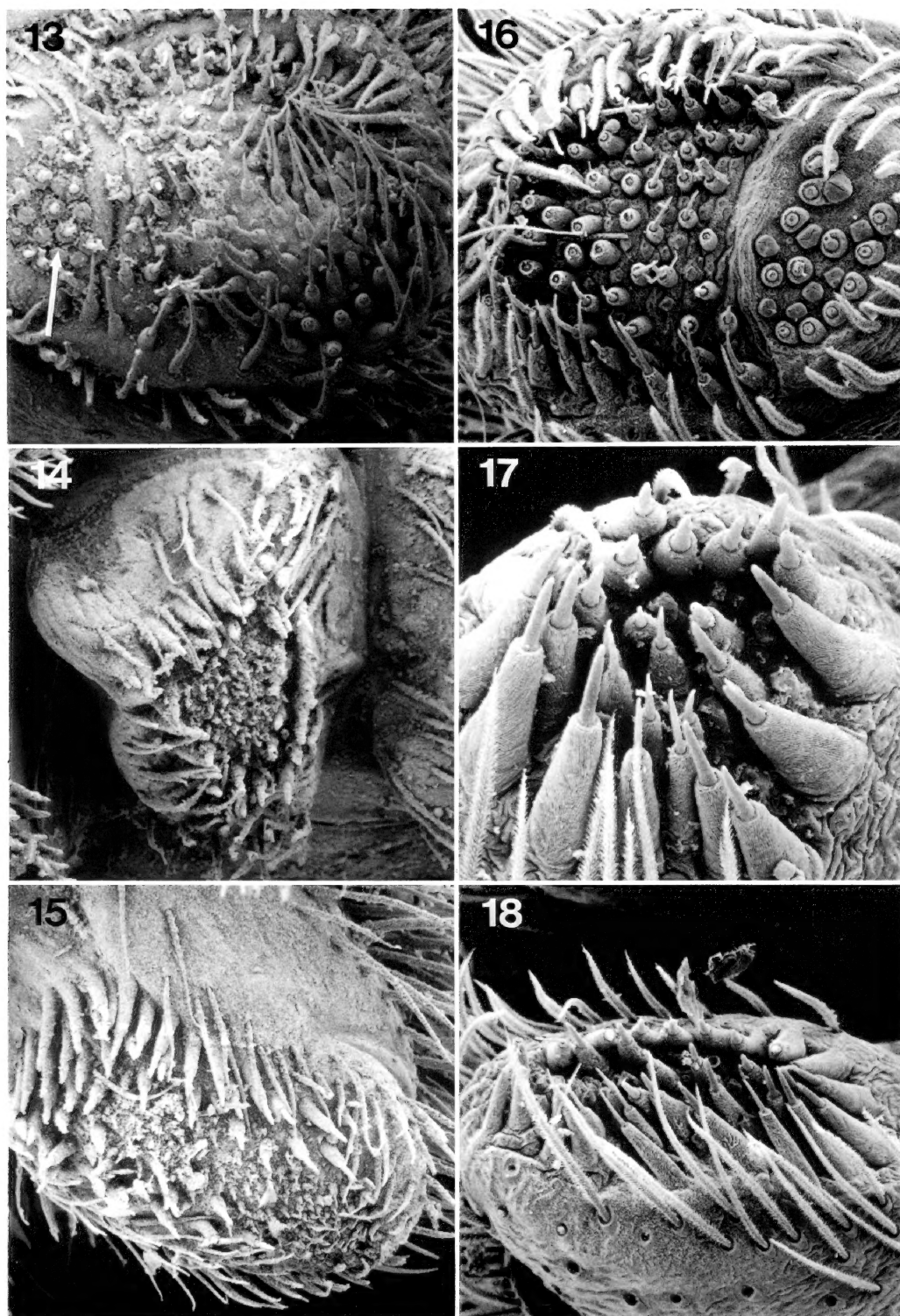
Figs. 13–18. *Gradungula sorenseni* Forster. 13–15. Female. 16–18. Male. **13, 16.** ALS, 280× (arrow to major ampullate gland spigot field), 375×. **14, 17.** PMS, 220×, 775×. **15, 18.** PLS, 185×, 380×.
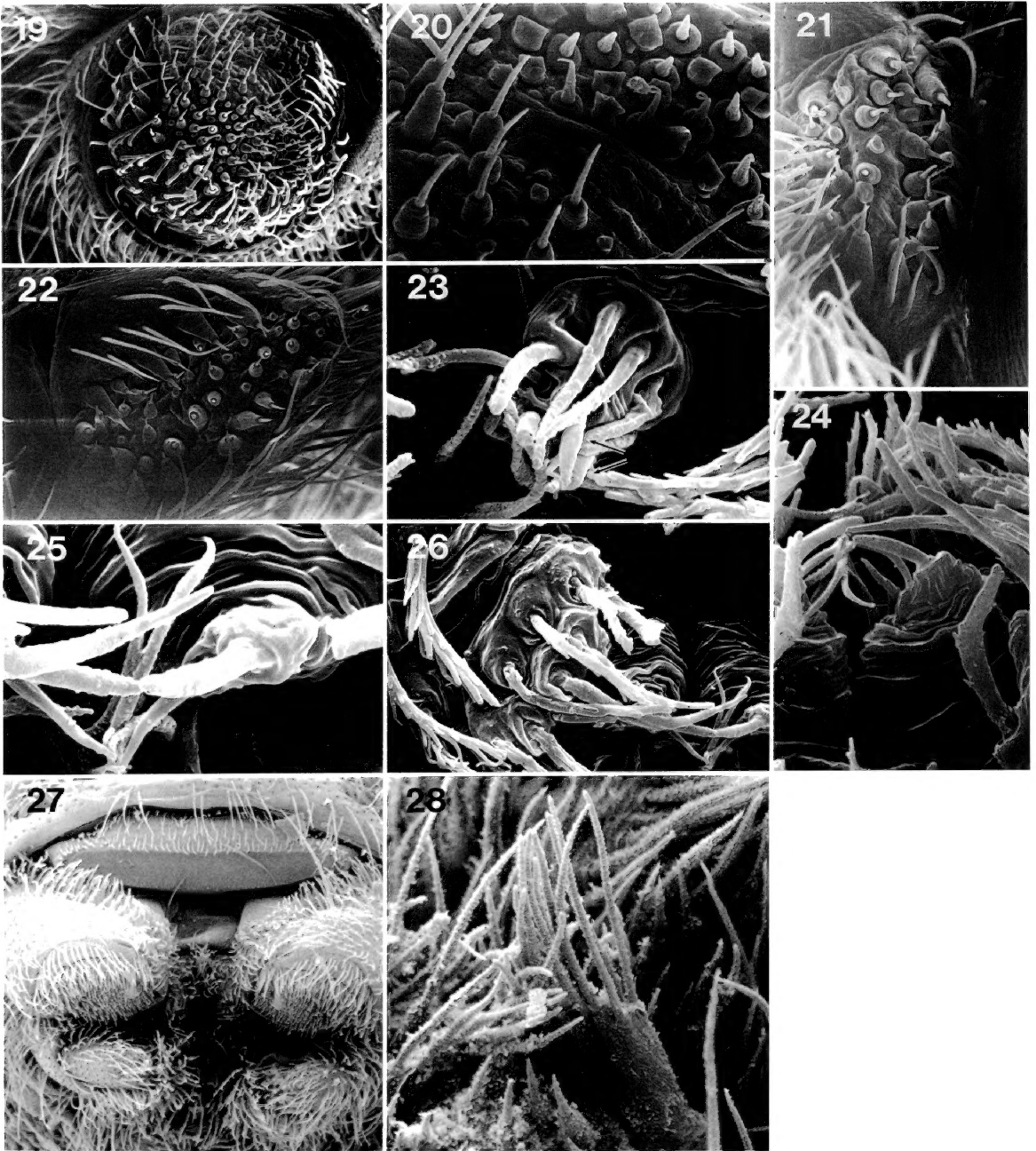
Figs. 19–28.   19–22. *Pianoa isolata* Forster, female. 23–26. Tetrablemmidae, female from Singapore. 27–28. *Austrochilus melon* Platnick. **19, 23.** ALS, 135×, 6100×. **20.** ALS major ampullate gland spigots, 460×. **21, 24, 25.** PMS, 340×, 3800×, 7500×. **22, 26.** PLS, 200×, 2900×. **27.** Spinning field of male, showing undivided cribellum, 75×. **28.** PMS paracribellar spigots of female, with multiple shafts arising from a single base, 500×.
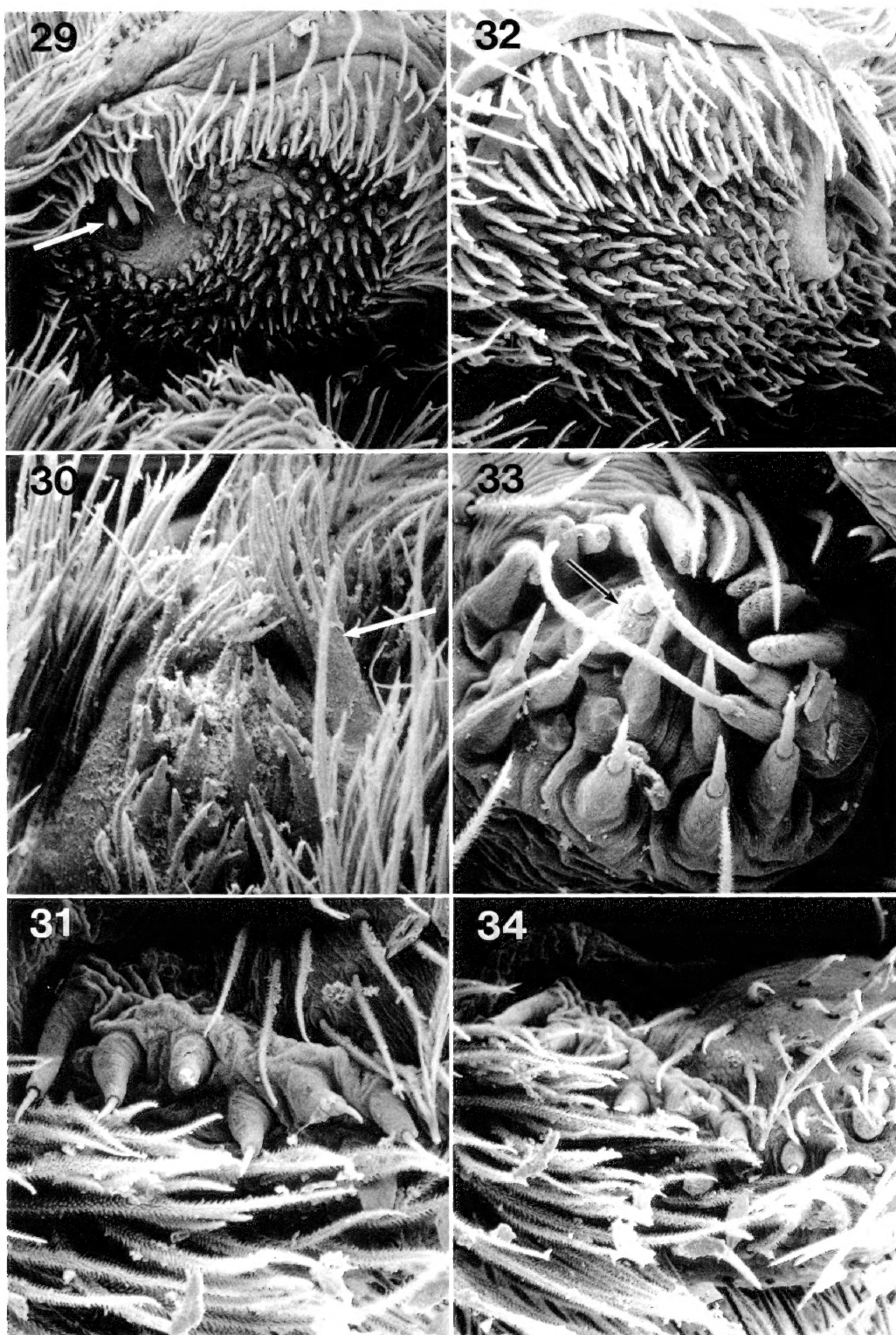
Figs. 29–34. *Austrochilus melon* Platnick. 29–31. Female. 32–34. Male. **29, 32.** ALS, 220× (arrow to major ampullate gland spigots), 330×. **30, 33.** PMS, 300× (arrow to base of paracribellar spigots), 765× (arrow to presumed minor ampullate gland spigots). **31, 34.** PLS, 500×, 380×.
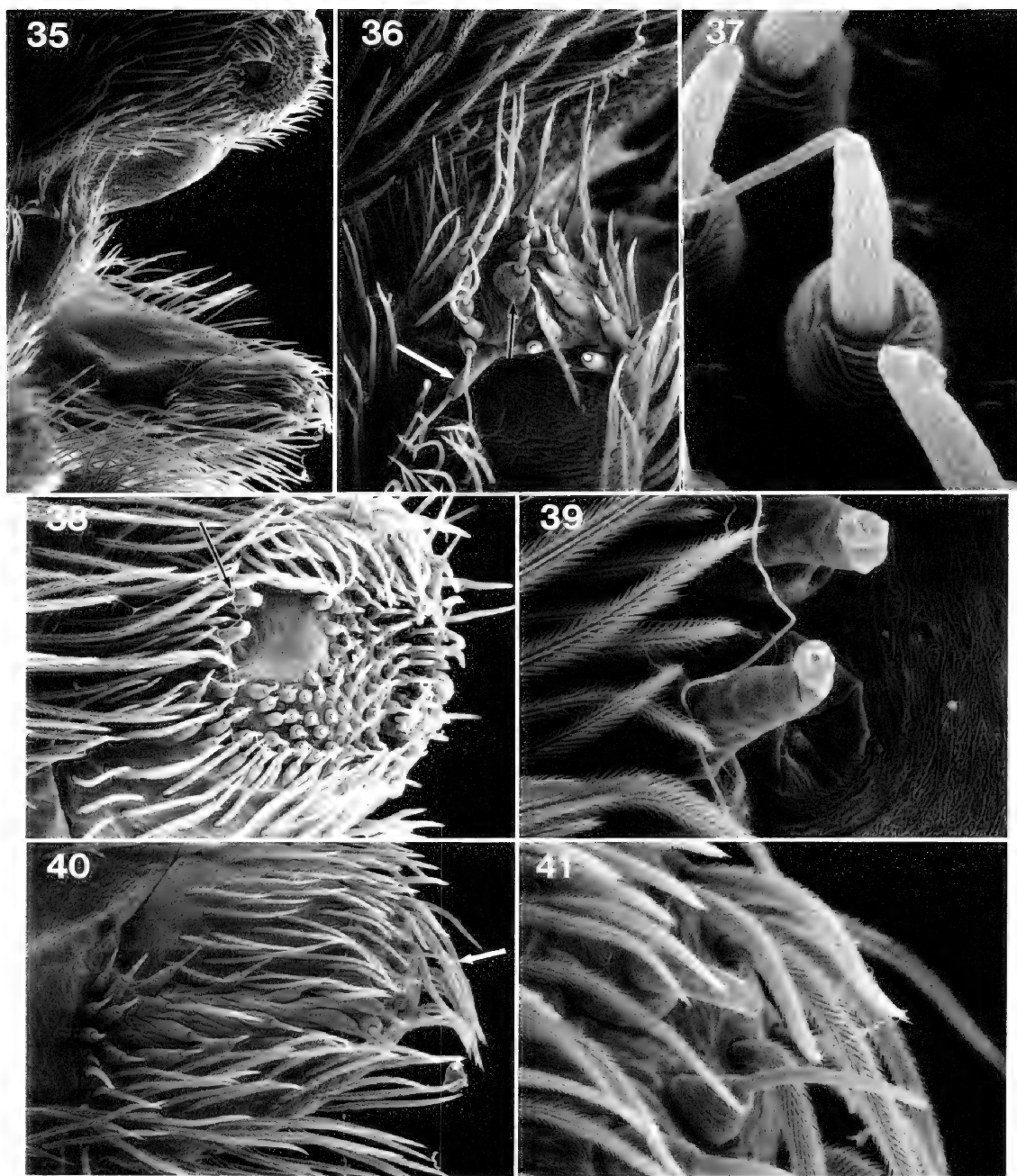
Figs. 35–41. *Thaida peculiaris* Karsch, female. **35.** Spinning field, left half, 110×. **36.** PMS, 330× (white arrow to single-shafted paracribellar spigot, black arrow to minor ampullate gland spigot). **37.** ALS piriform gland spigots, 4500×. **38.** ALS, 325× (arrow to major ampullate gland spigots). **39.** ALS major ampullate gland spigots, 1525×. **40.** PLS, 280× (arrow to paracribellar spigot). **41.** PLS paracribellar spigot, 1100×.
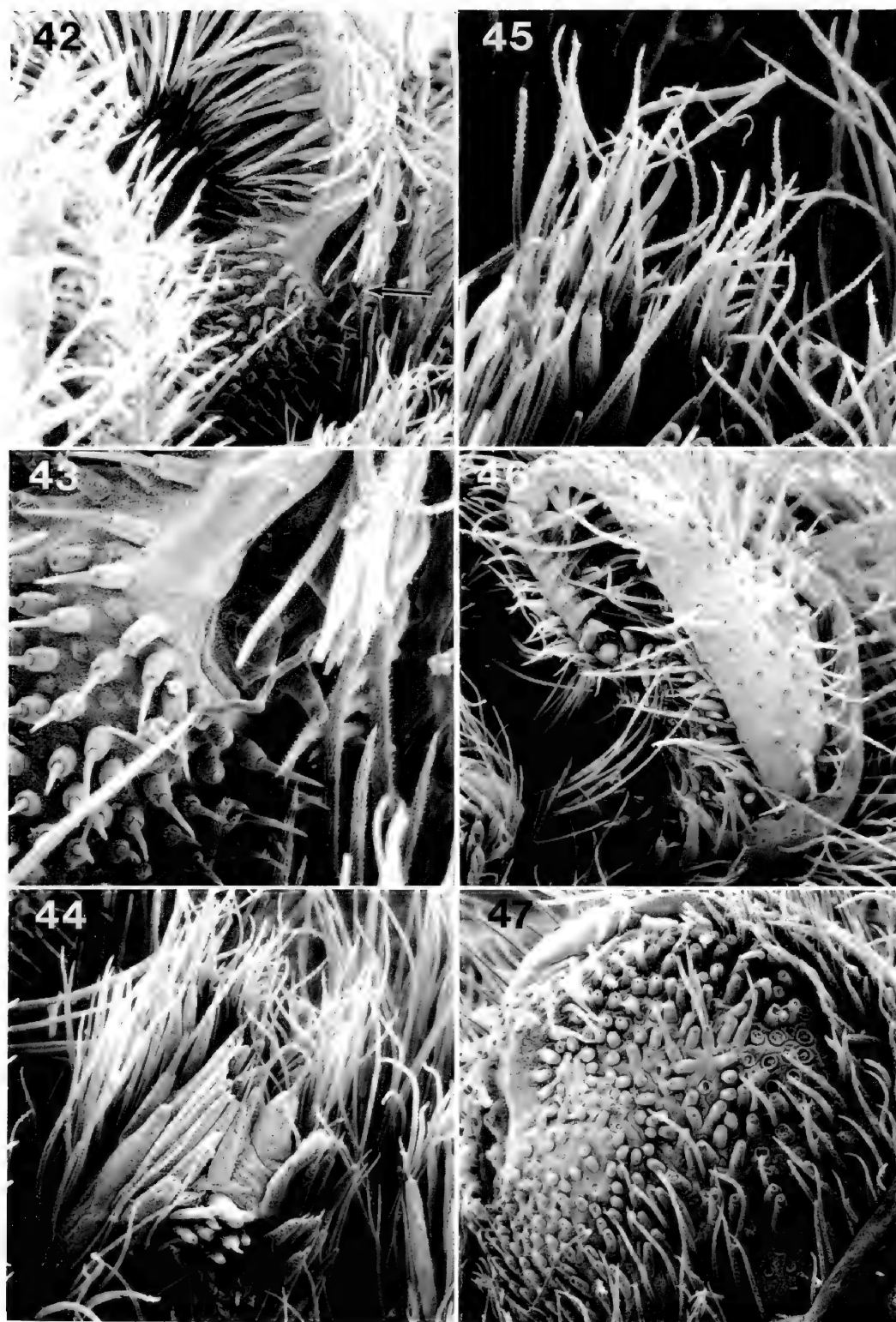
Figs. 42–47. *Hickmania troglodytes* (Higgins and Petterd). 42–46. Female. 47. Male. **42, 47.** ALS, 185× (arrow to major ampullate gland spigots), 220×. **43.** ALS major ampullate gland spigots, 475×. **44.** PMS, 240×. **45.** PMS paracribellar spigots, 500×. **46.** PLS, 135×.
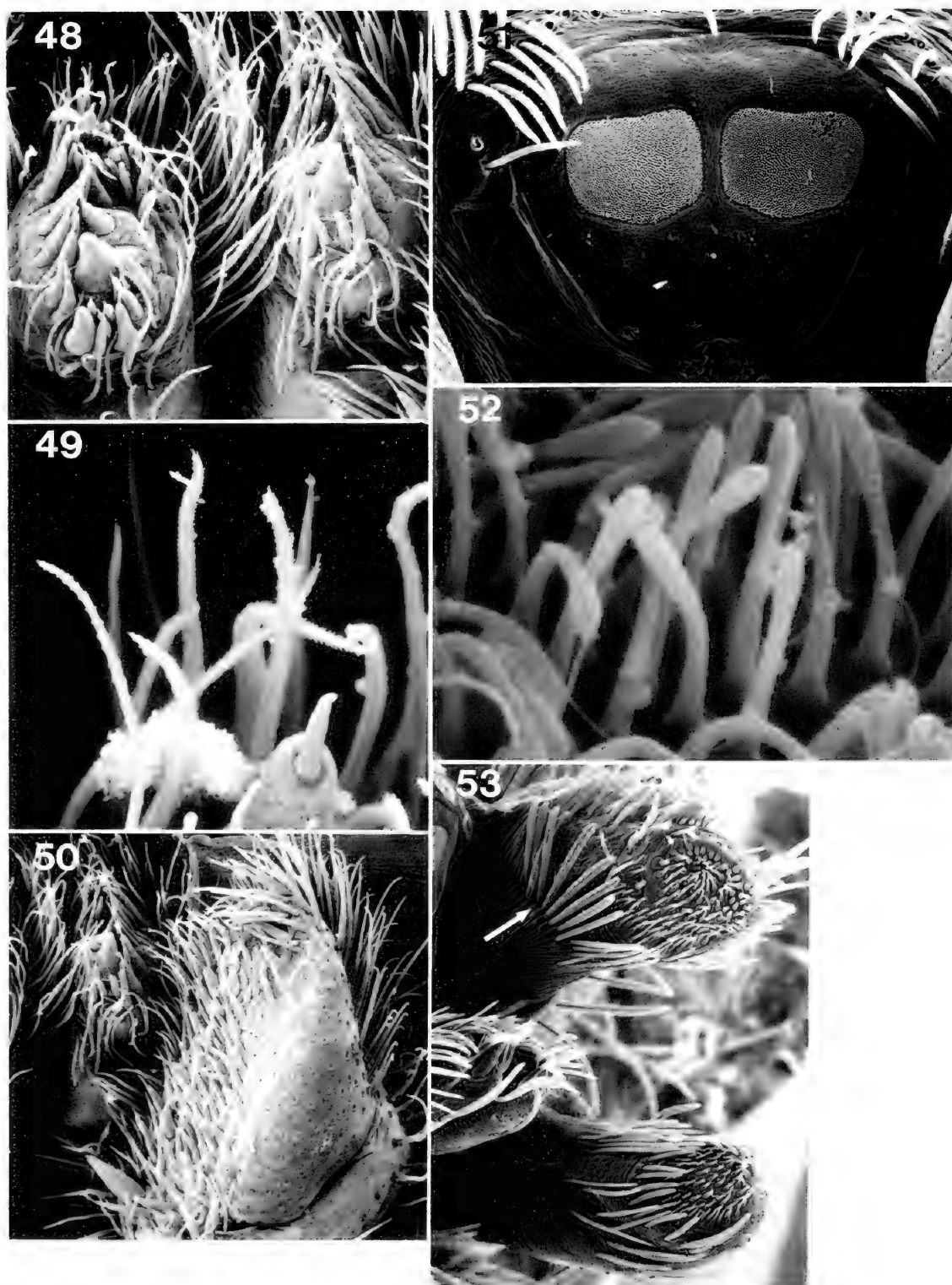
Figs. 48–53.   48–50. *Hickmania troglodytes* (Higgins and Petterd), male. 51–53. *Kukulcania hibernalis* (Hentz), female. **48.** PMS, 240×. **49.** PMS paracribellar spigots, 1290×. **50.** PLS, 145×. **51.** Divided cribellum, 265×. **52.** Cribellar spigots, 9400×. **53.** Left spinning field, 135× (arrow to row of specialized setae).
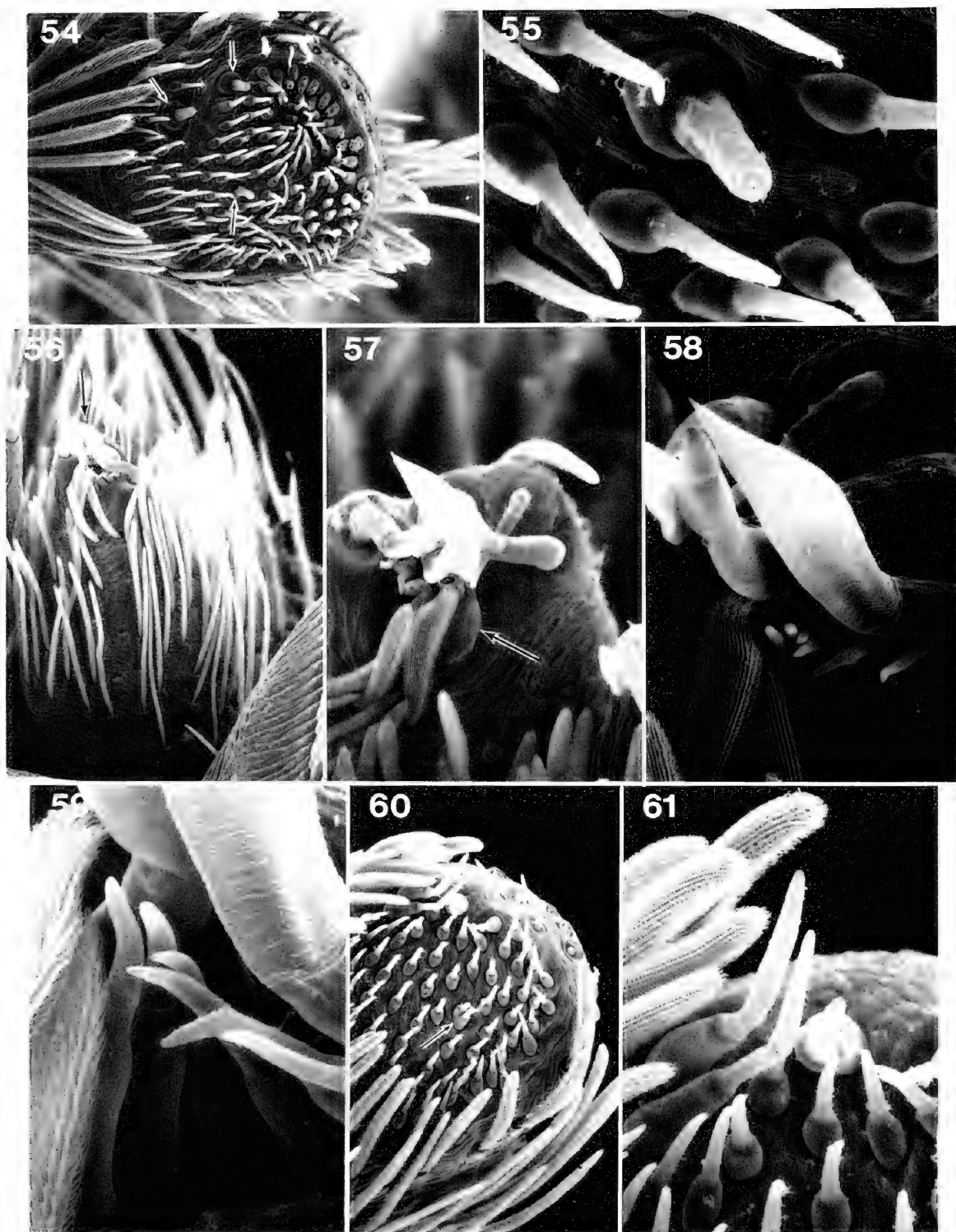
Figs. 54–61. *Kukulcania hibernalis* (Hentz), female. **54.** ALS, 290× (arrows to major ampullate gland spigots). **55.** One of the major ampullate gland spigots, situated among within the piriform gland spigot field, 1950×. **56.** PMS, 250× (arrow to paracribellar spigots). **57, 58.** PMS spigots, showing enlarged probable minor ampullate gland spigot (arrow) and paracribellar spigots as well as smaller aciniform gland spigots, 660×, 1075×. **59.** PMS aciniform gland spigots, 2500×. **60.** PLS, 405× (arrow to double-shafted spigot). **61.** PLS probable paracribellar spigots, 1300×.
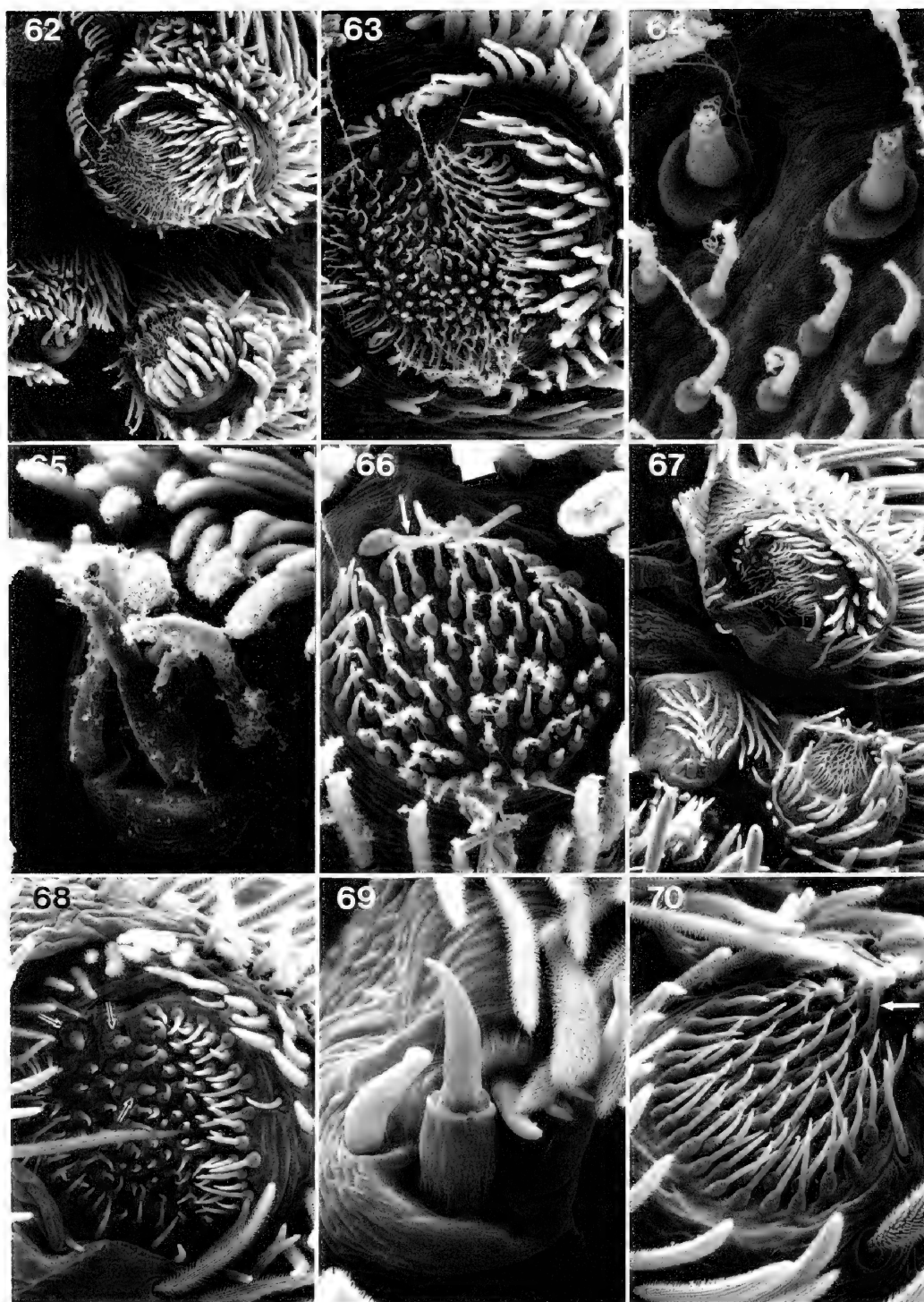
Figs. 62–70. *Filistata insidiatrix* (Forskal). 62–66. Female. 67–70. Male. **62, 67.** Left spinning field, 145×, 225×. **63, 68.** ALS, 325×, 620× (arrows to major ampullate gland spigots). **64.** Two of the ALS major ampullate gland spigots, 1575×. **65, 69.** PMS, 830×, 1550×. **66, 70.** PLS, showing probable paracribellar gland spigots (arrows), 720×, 940×.
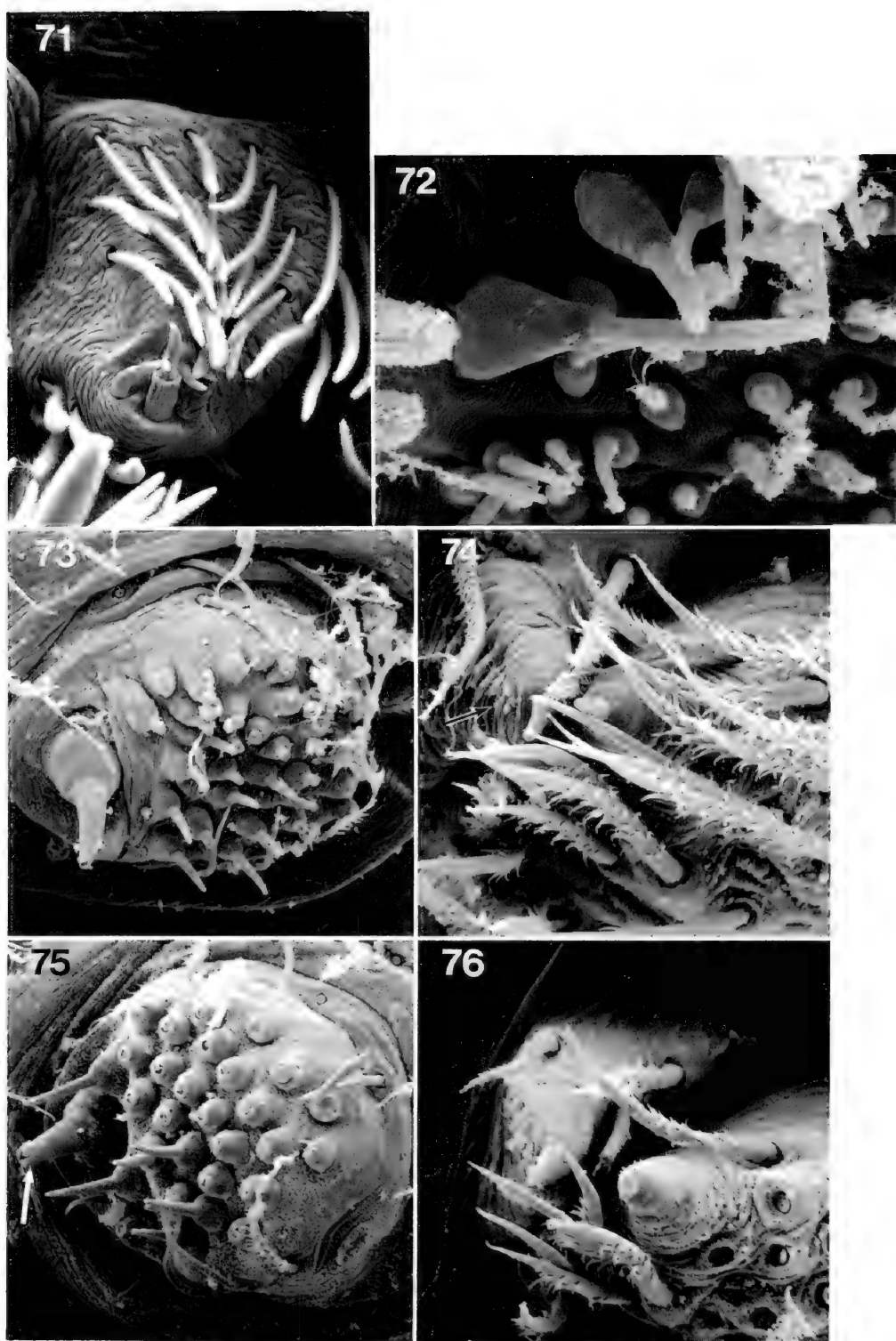
Figs. 71–76. 71, 72. *Filistata insidiatrix* (Forskal). 73–76. *Scytodes* sp. (Texas). **71.** Male, PMS, showing three probable paracribellar spigots, one probable minor ampullate gland spigot, and three probable aciniform gland spigots, 550×. **72.** Female, PLS, probable paracribellar spigot, 1800×. **73, 75.** ALS, female and male, 570×, 670× (arrow to major ampullate gland spigot). **74, 76.** PMS and PLS, female and male, 1000× (arrow to spicules), 935×.
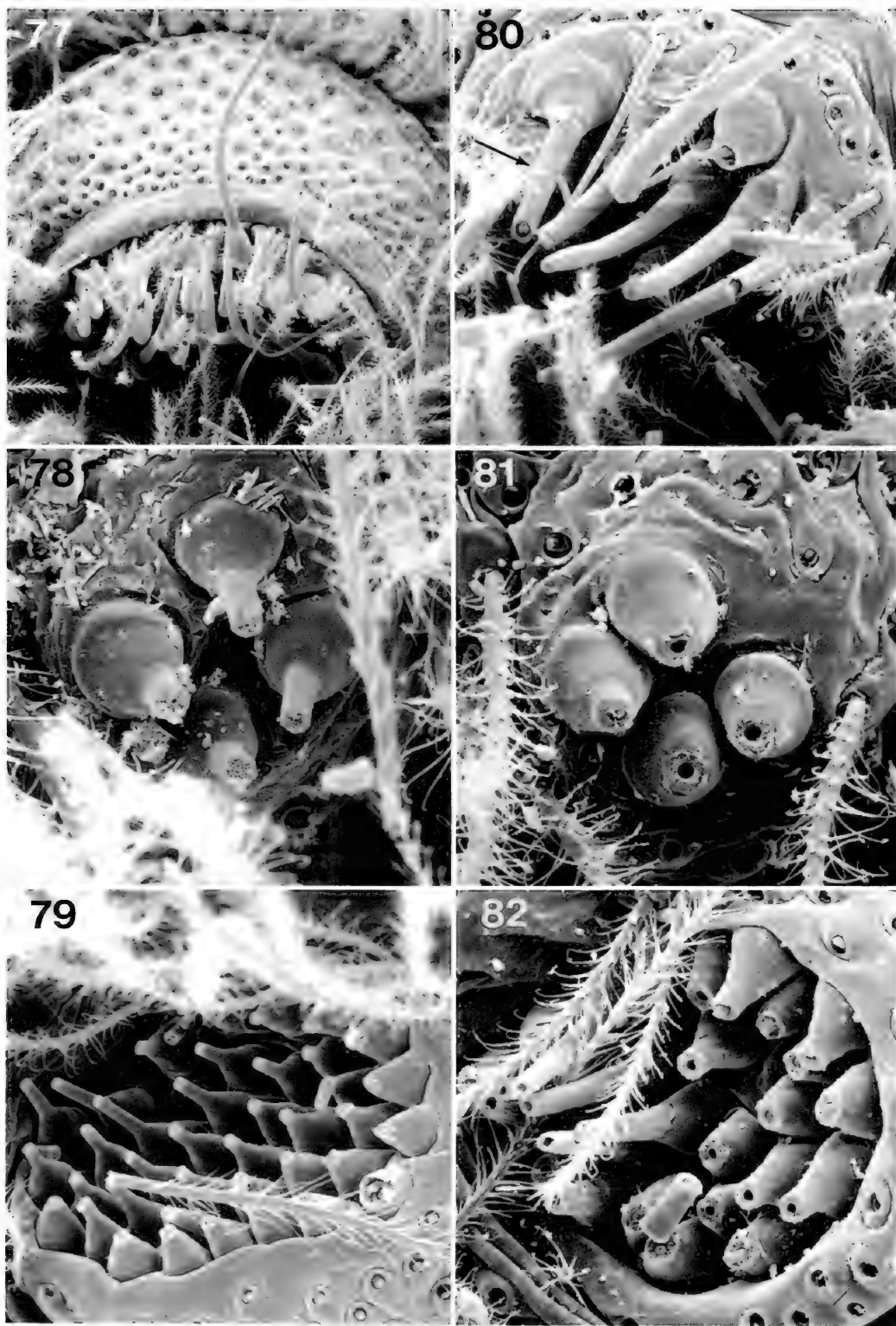
Figs. 77–82. *Sicarius* sp. (Chile). 77–79. Female. 80–82. Male. **77, 80.** ALS, 185×, 500×. **78, 81.** PMS, 910×, 1000×. **79, 82.** PLS, 475×, 760×.
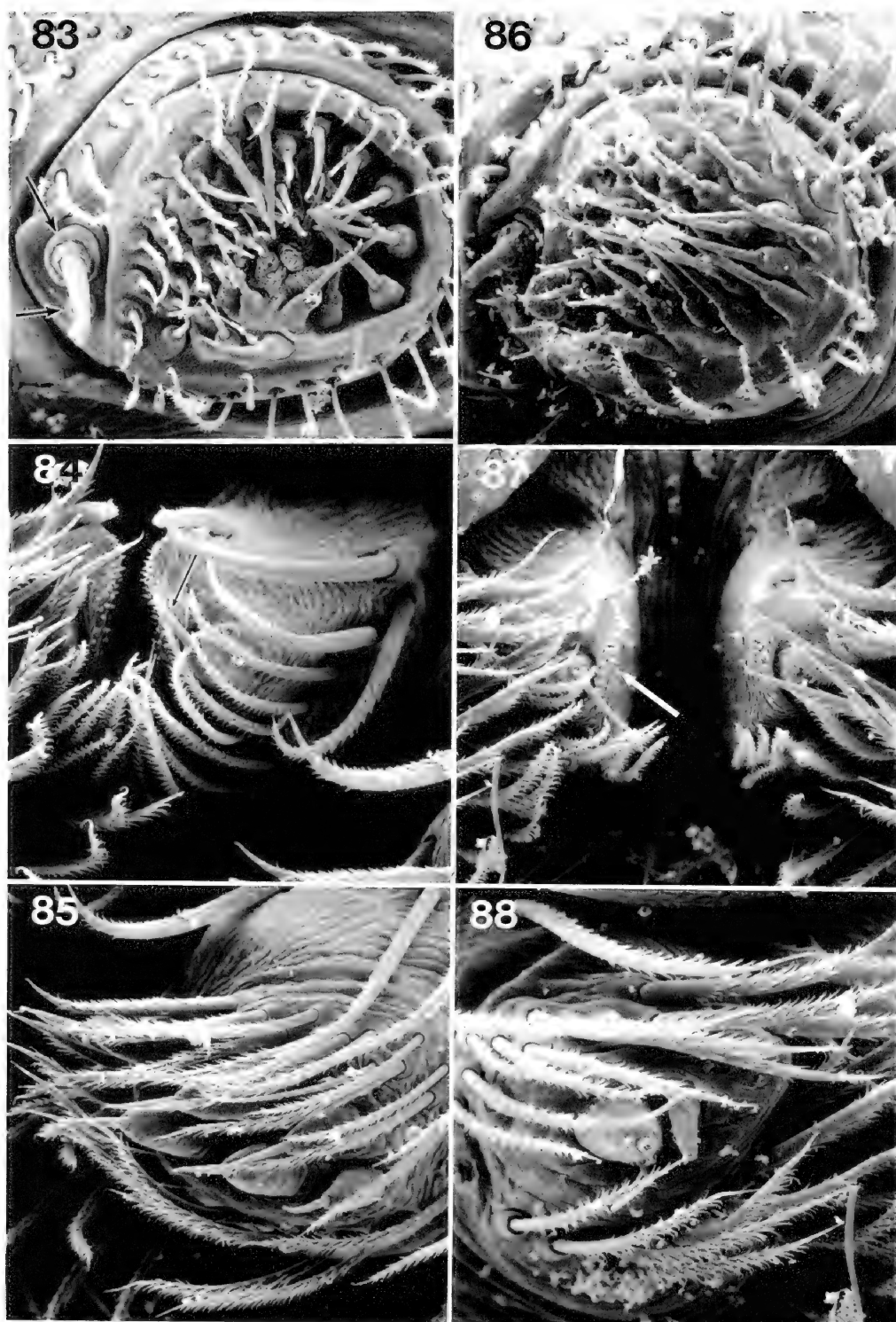
Figs. 83–88. *Drymusa* sp. (South Africa). 83–85. Female. 86–88. Male. **83, 86.** ALS, 405× (upper arrow to major ampullate gland spigot, lower arrow to partially hidden nubbin), 500×. **84, 87.** PMS, 500× (arrow to aciniform gland spigot shaft), 470× (arrow to spicules). **85, 88.** PLS, 390×, 610×.
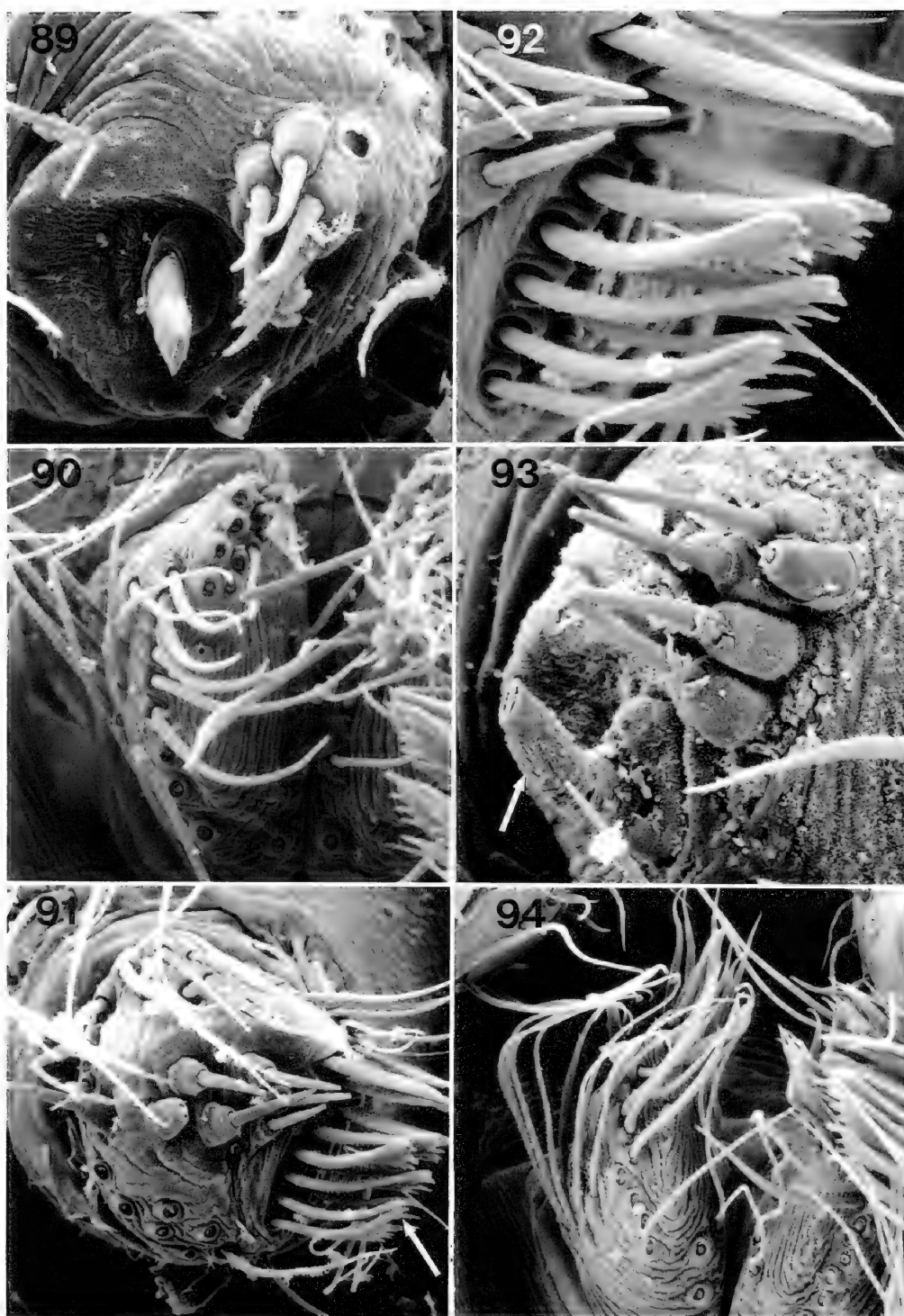
Figs. 89–94. *Loxosceles reclusa* Gertsch and Mulaik. 89–92. Female. 93, 94. Male. **89, 93.** ALS, 1000×, 1430× (arrow to major ampullate gland spigot). **90, 94.** PMS, 625×, 500×. **91.** PLS, 525× (arrow to modified setae). **92.** PLS modified setae, 1150×.
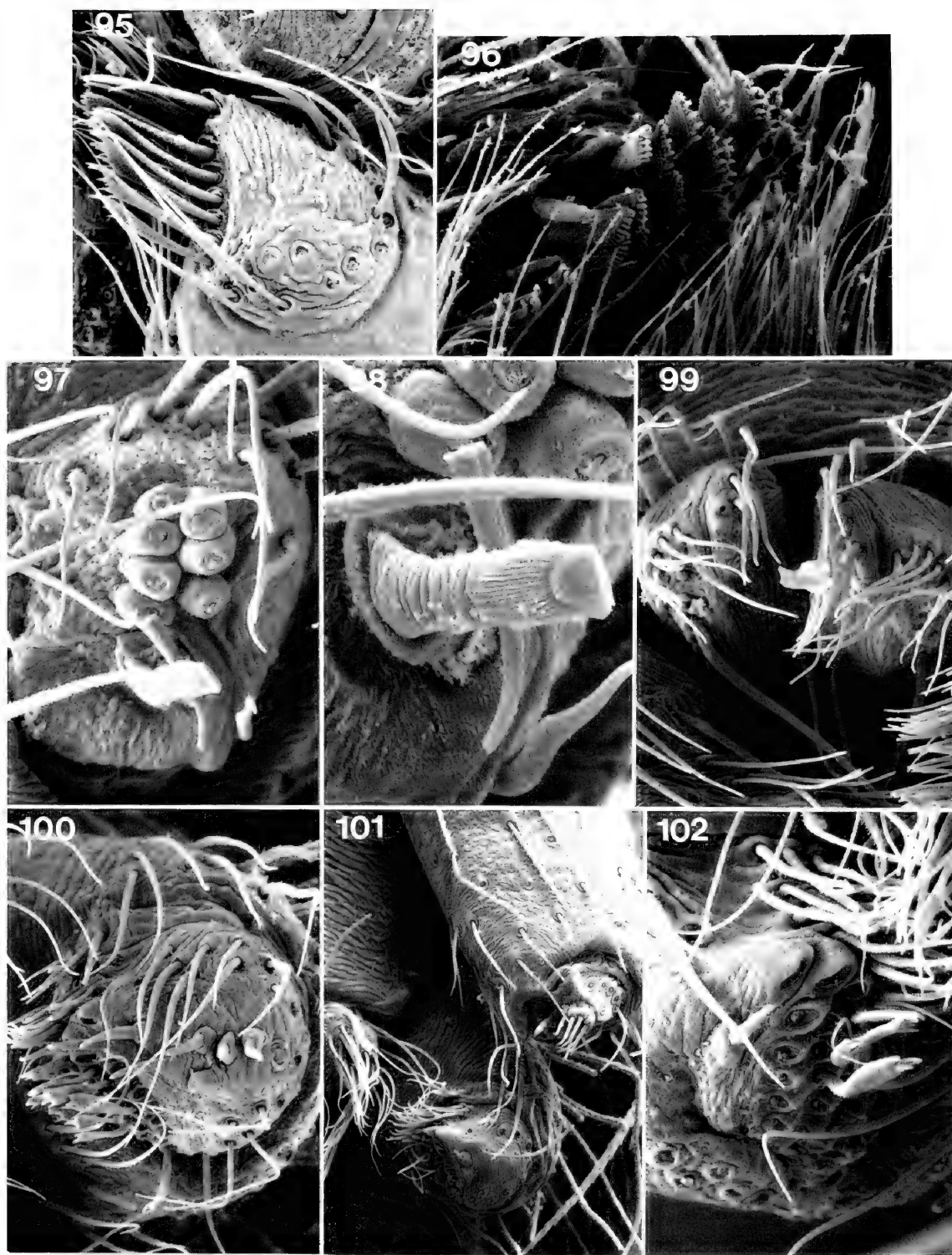
Figs. 95–102. 95. *Loxosceles reclusa* Gertsch and Mulaik. 96. *L. laeta* (Nicolet). 97–102. *L. rufescens* (Dufour). 95, 101, 102. Male. 96–100. Female. **95, 96, 100, 102.** PLS, 615×, 425×, 560×, 1275×. **97.** ALS, 1050×. **98.** ALS major ampullate gland spigot, 2275×. **99.** PMS, 540×. **101.** Left spinning field, 340×.
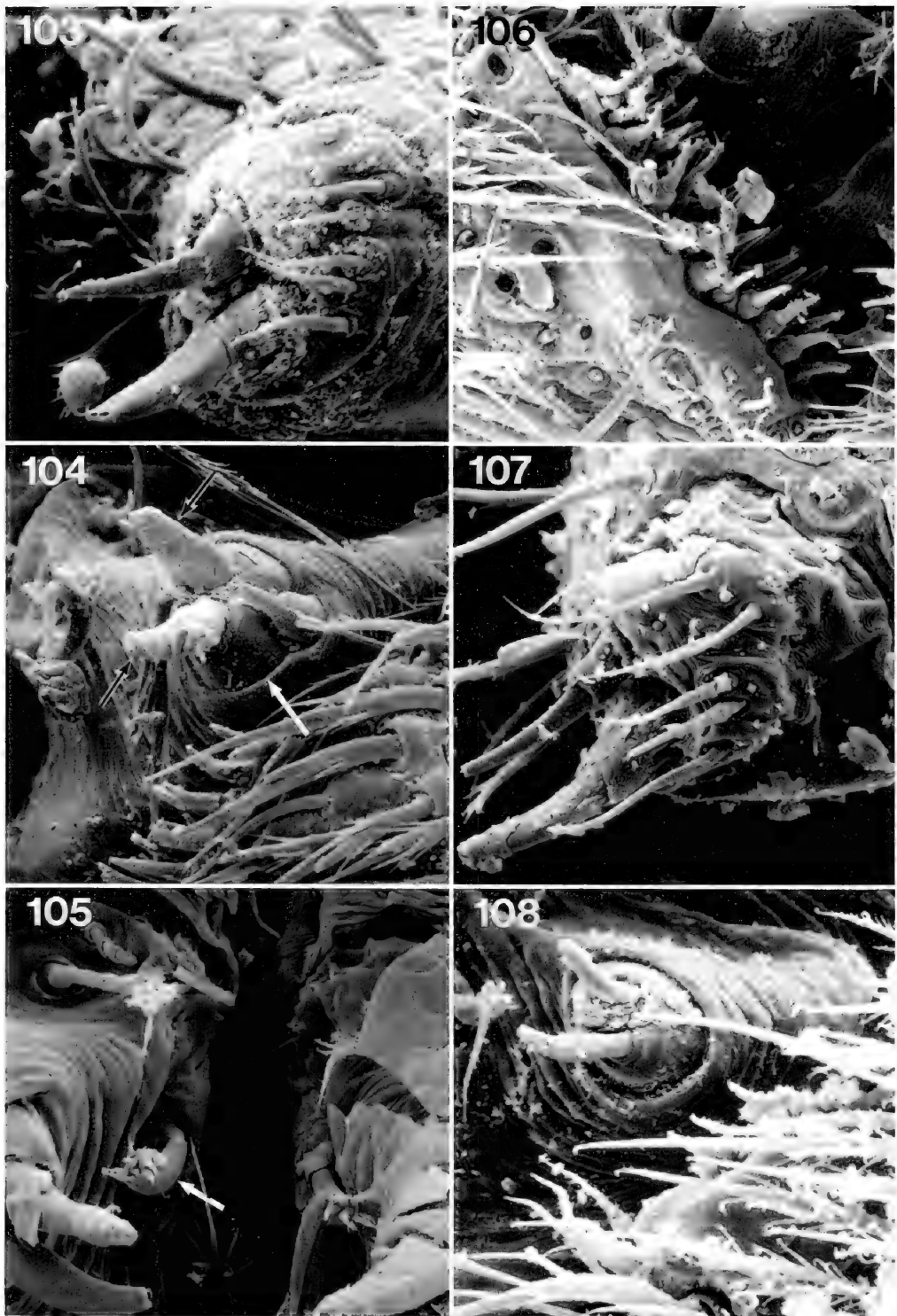
Figs. 103–108.　*Diguetia* sp. (United States). 103–106. Female. 107, 108. Male. **103, 107.** ALS, 870×, 1110×. **104, 108.** PMS, 610× (black arrows to presumed minor ampullate gland spigots, white arrow to distal ring formed by fused spigot bases), 1205×. **105.** Modified setae on PMS base (arrow), 1135×. **106.** PLS, 500×.
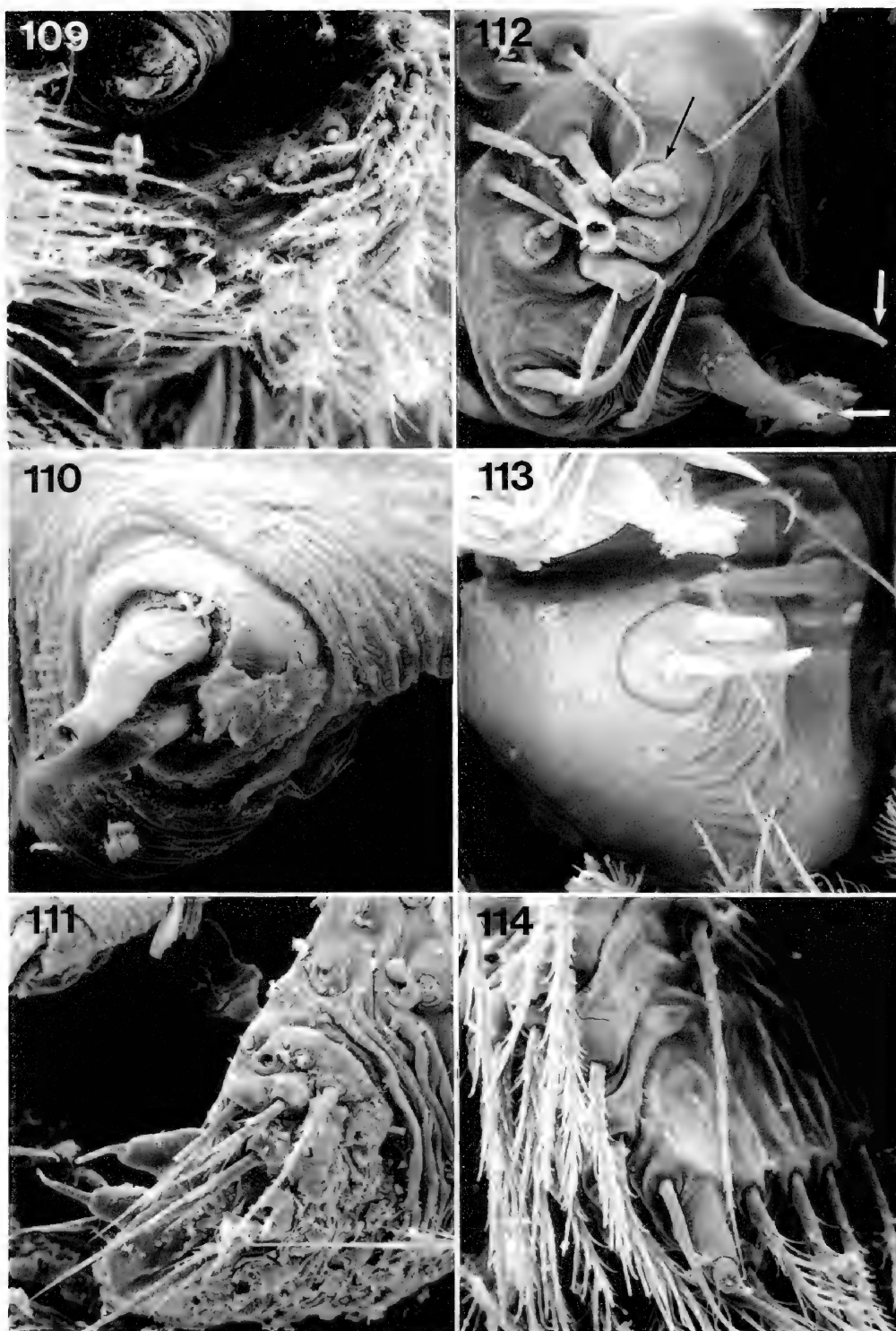
Figs. 109–114. 109–111. *Diguetia* sp. (United States), males. 112–114. *Segestrioides tofo* Platnick, female. **109, 111, 114.** PLS, 755×, 735×, 1000×. **110, 113.** PMS, 2000×, 1000×. **112.** ALS, 1230× (white arrows to major ampullate gland spigots, black arrow to piriform gland spigot).
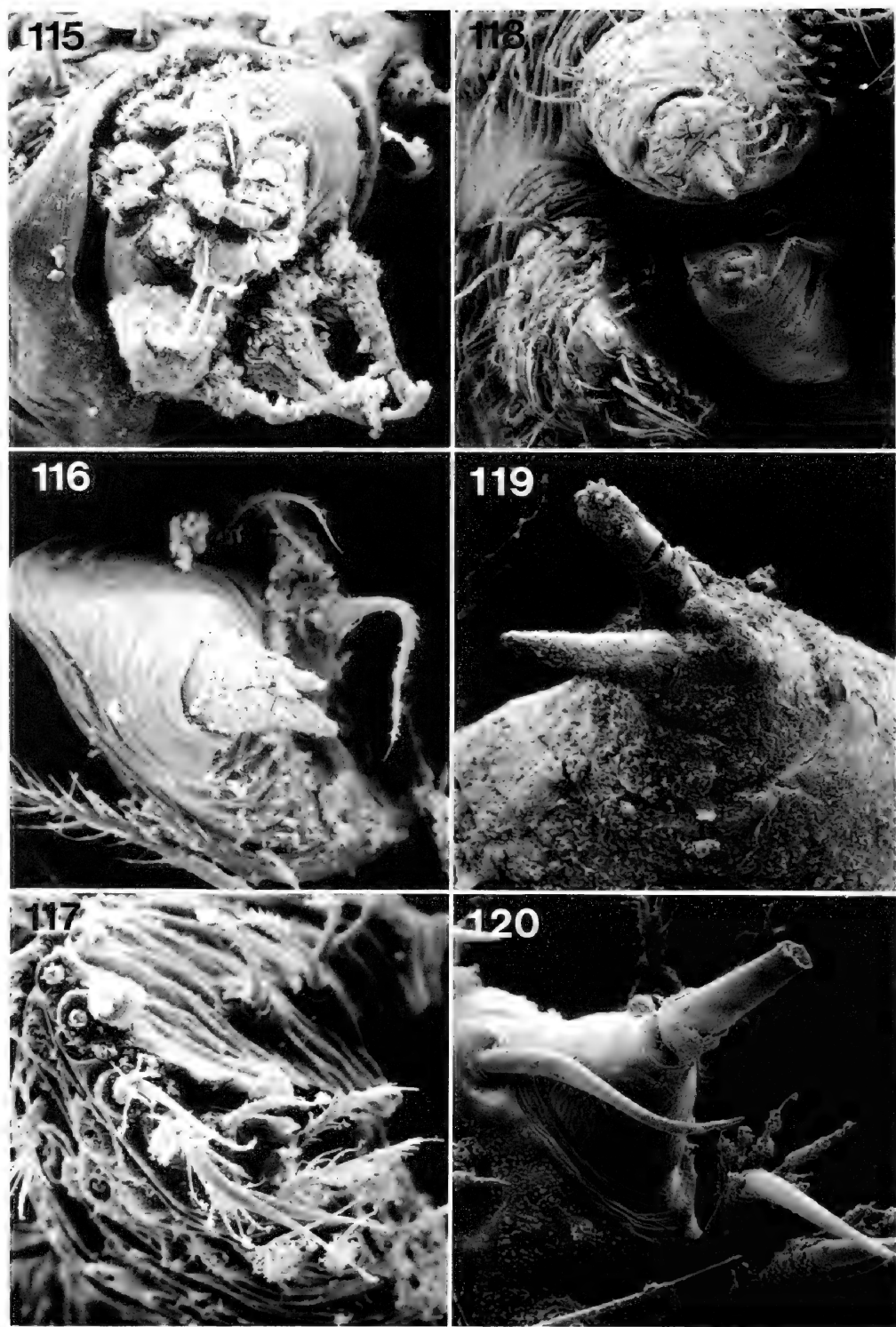
Figs. 115–120.   115–117. *Segestrioides tofo* Platnick, male. 118–120. *S. bicolor* Keyserling, female. **115.** ALS, 1000×. **116, 119.** PMS, 1000×, 1000×. **117, 120.** PLS, 1225×. **118.** Right spinning field, 200×.
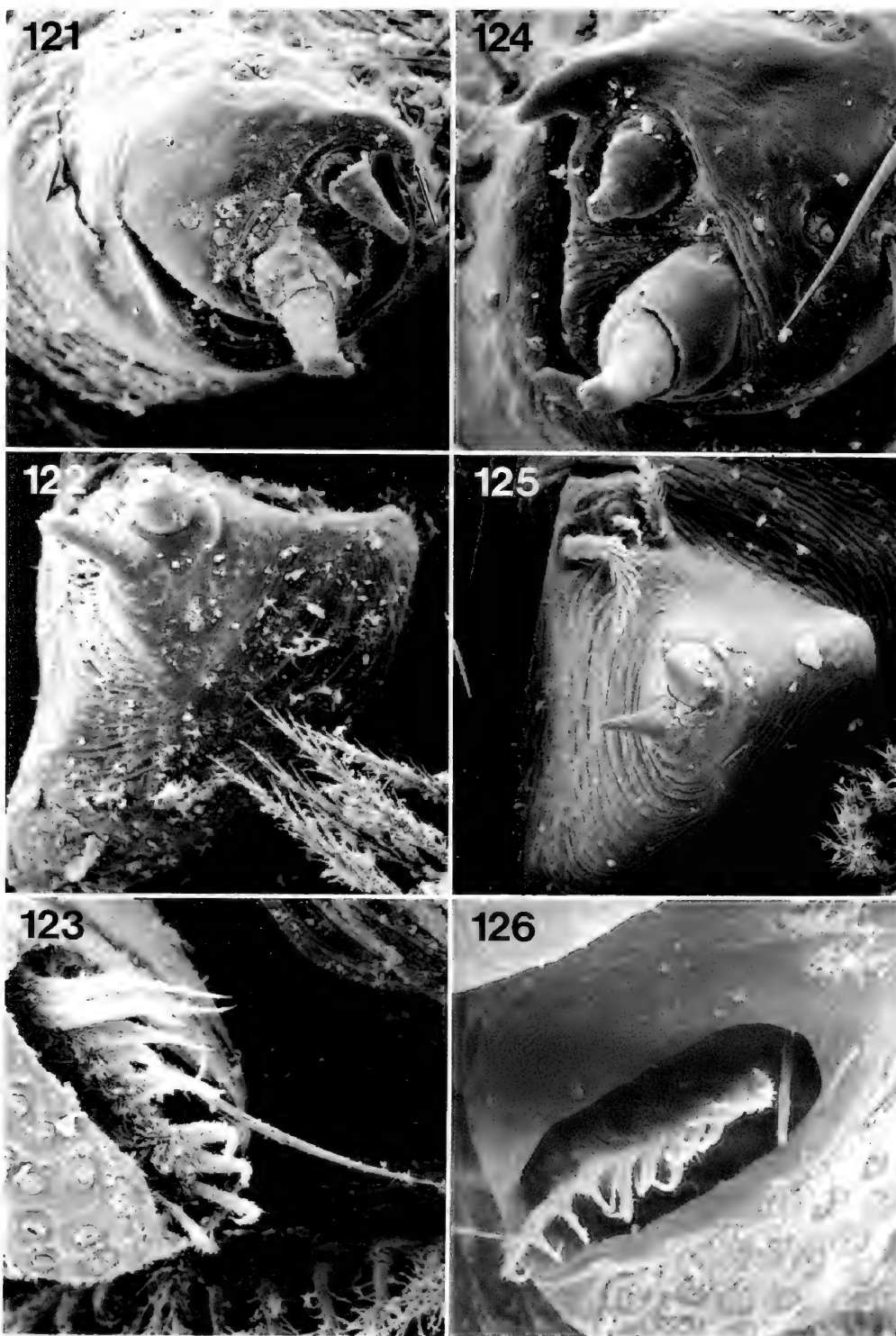
Figs. 121–126. *Plectreurys tristis* Simon. 121–123. Female. 124–126. Male. **121, 124.** ALS, 500× (arrow to hook), 1000×. **122, 125.** PMS, 500×, 500×. **123, 126.** PLS, 415×, 560×.
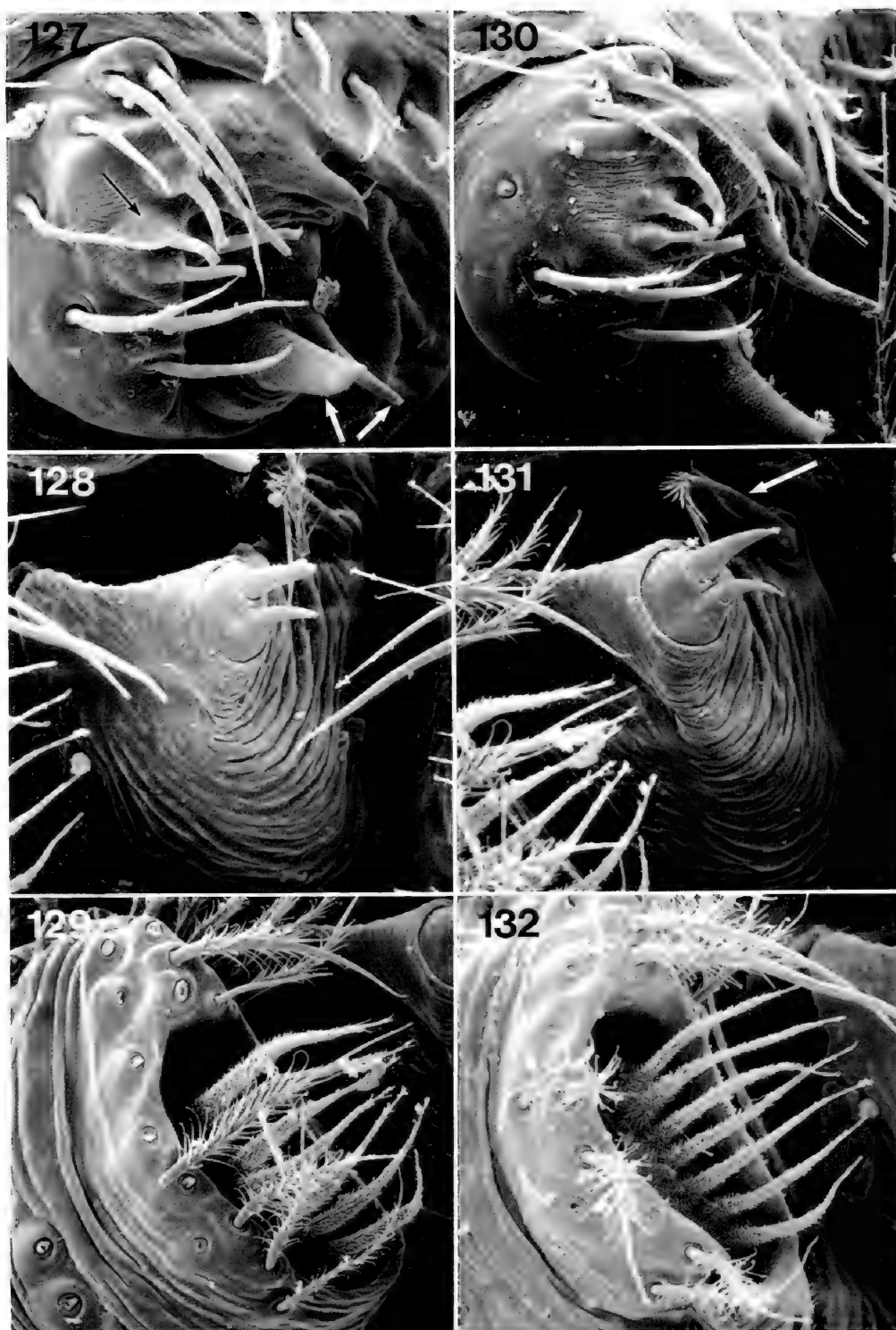
Figs. 127–132. *Kibramoa suprenans* Chamberlin. 127–129. Female. 130–132. Male. **127, 130.** ALS, 1000× (white arrows to major ampullate gland spigots, black arrow to piriform gland spigot), 1000× (arrow to hook). **128, 131.** PMS, 595×, 700× (arrow to modified seta). **129, 132.** PLS, 500×, 635×.
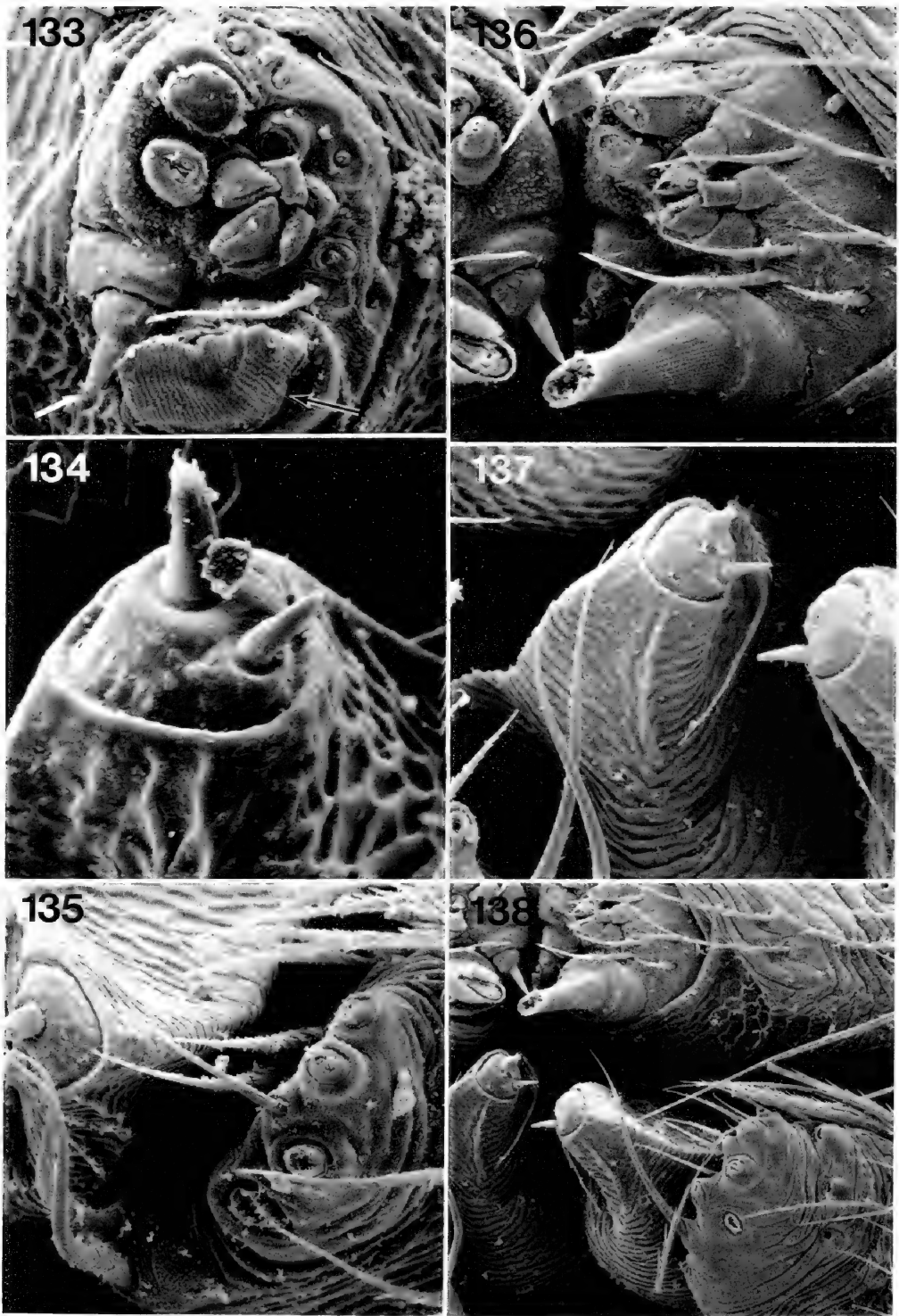
Figs. 133–138. *Pholcus phalangioides* (Fuesslin). 133–135. Female. 136–138. Male. **133, 136.** ALS, 1000× (black arrow to modified piriform gland spigot, white arrow to major ampullate gland spigot), 850×. **134, 137.** PMS, 2000×, 850×. **135, 138.** PLS (and PMS), 925×, 405×.
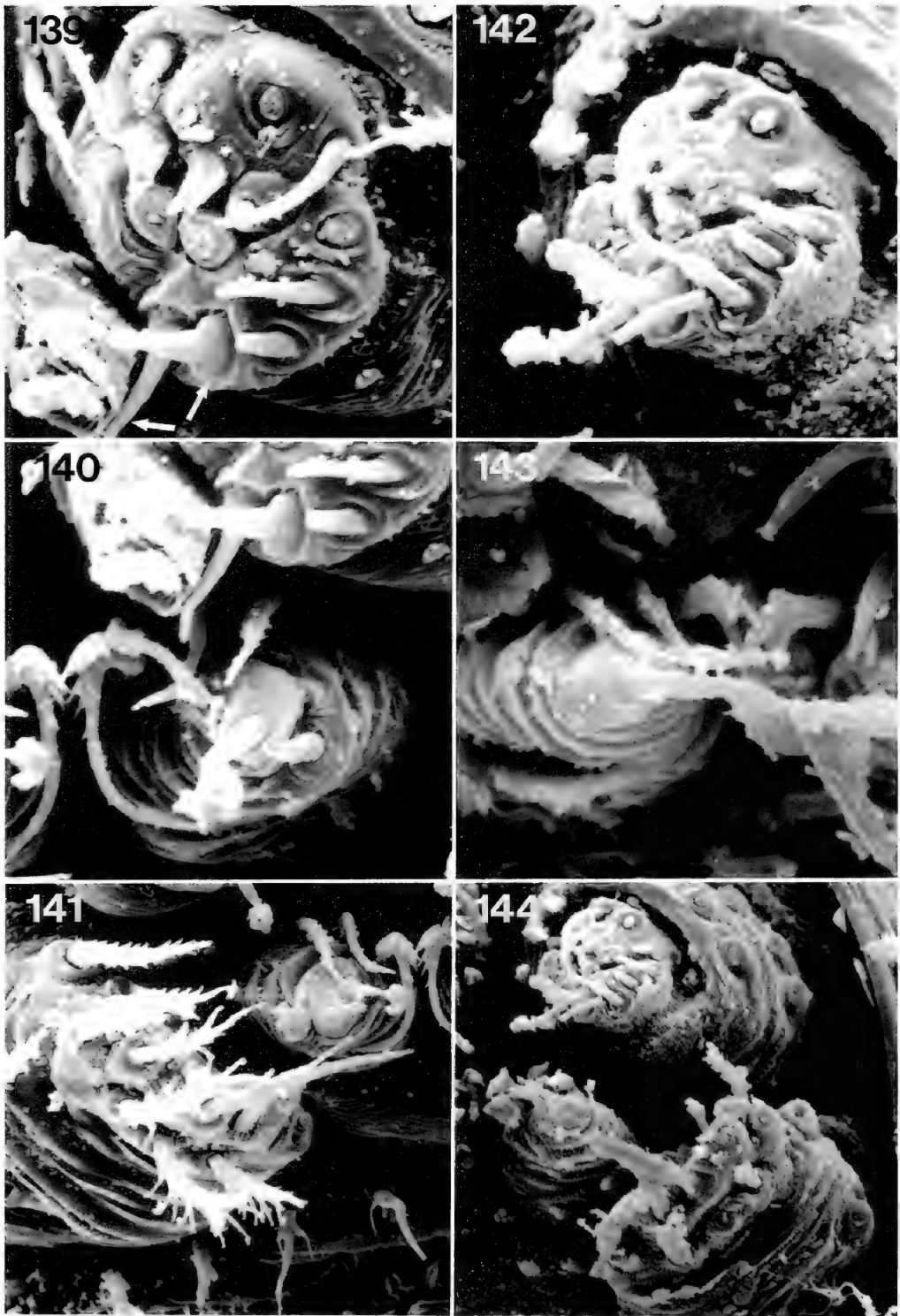
Figs. 139–144. *Caraimatta sbordonii* (Brignoli). 139–141. Female. 142–144. Male. **139, 142.** ALS, 5180× (arrows to major ampullate gland spigots), 5000×. **140, 143.** PMS, 5000×, 6010×. **141, 144.** PLS (and PMS), 2930×, 2255×.
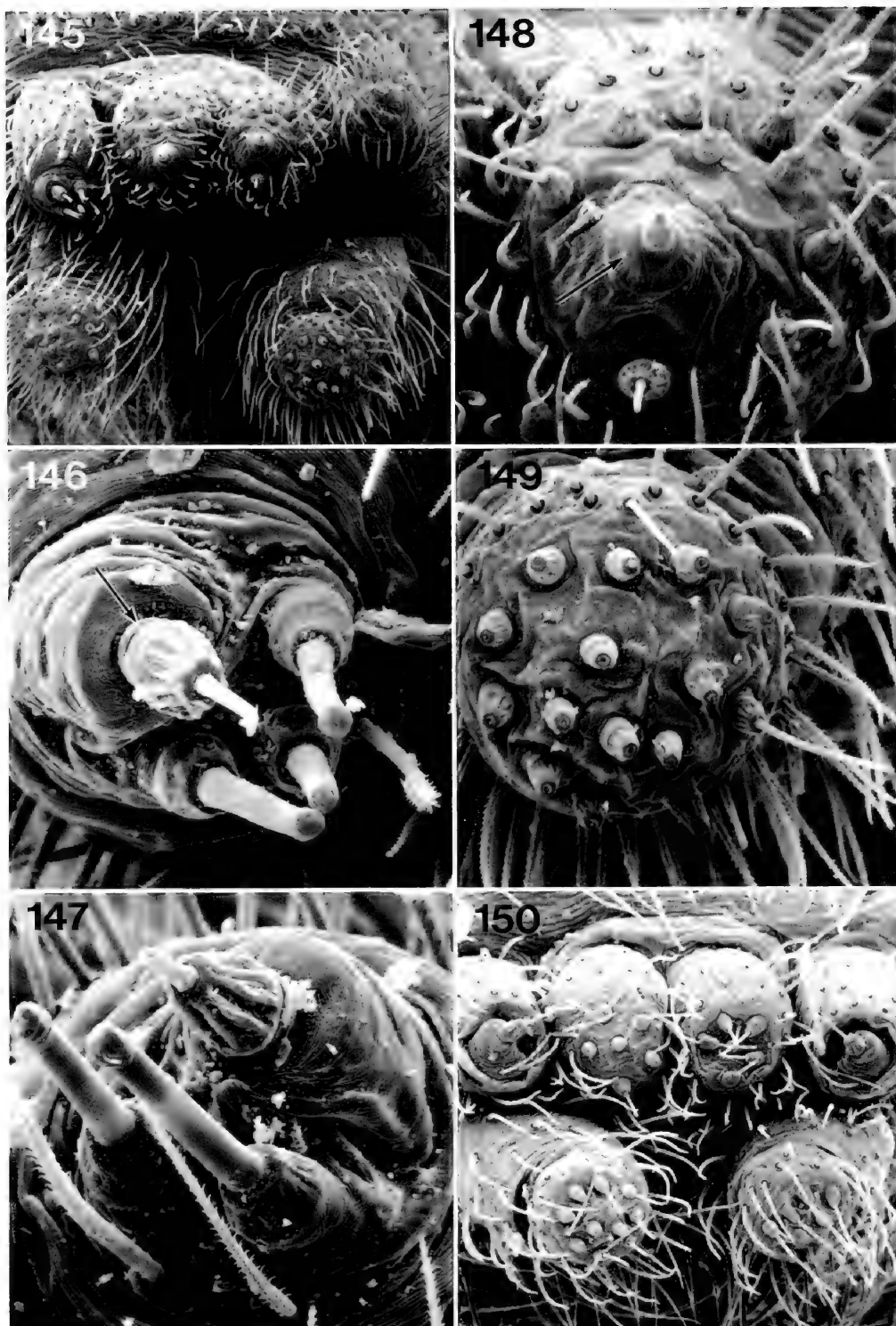
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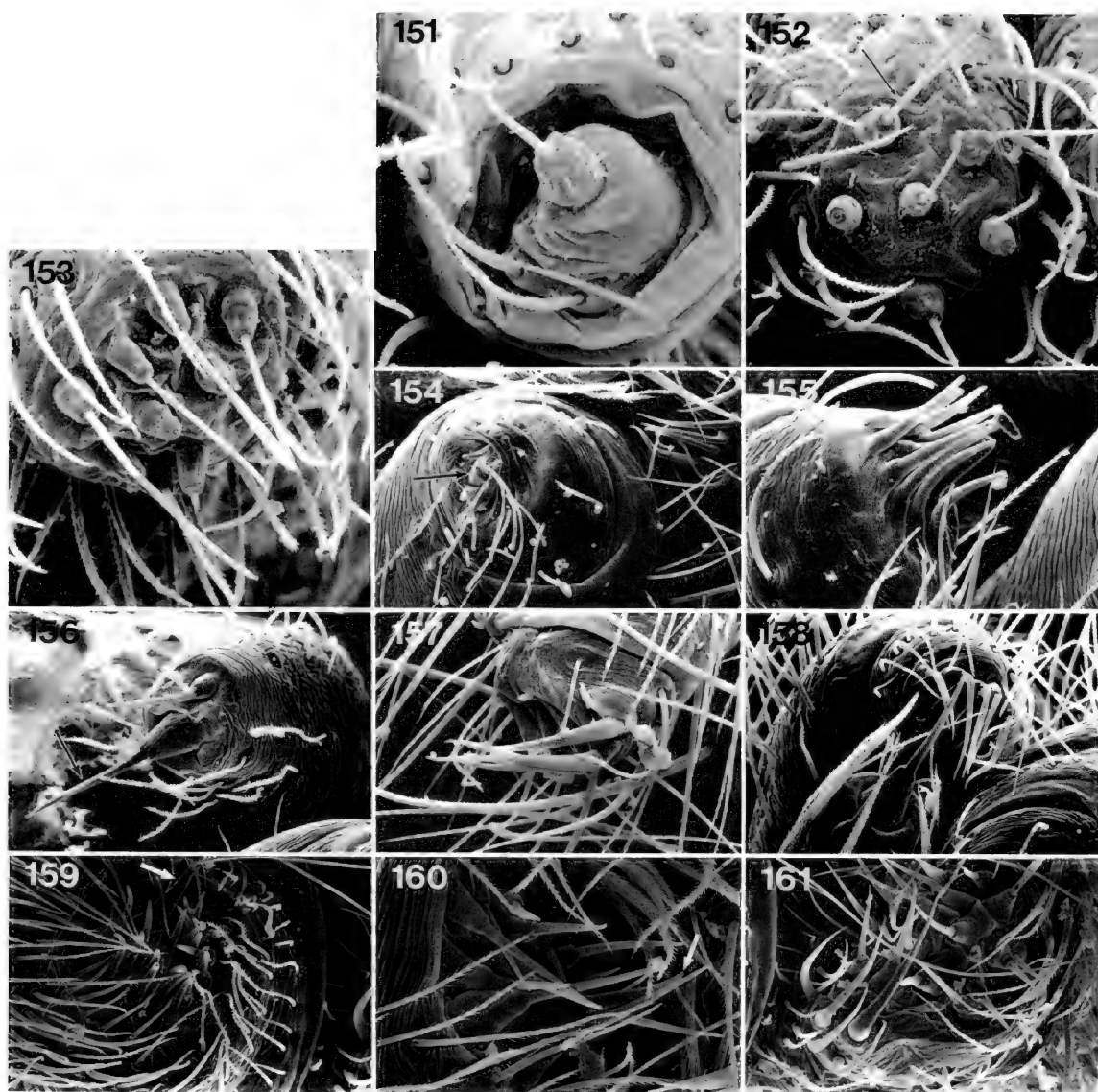
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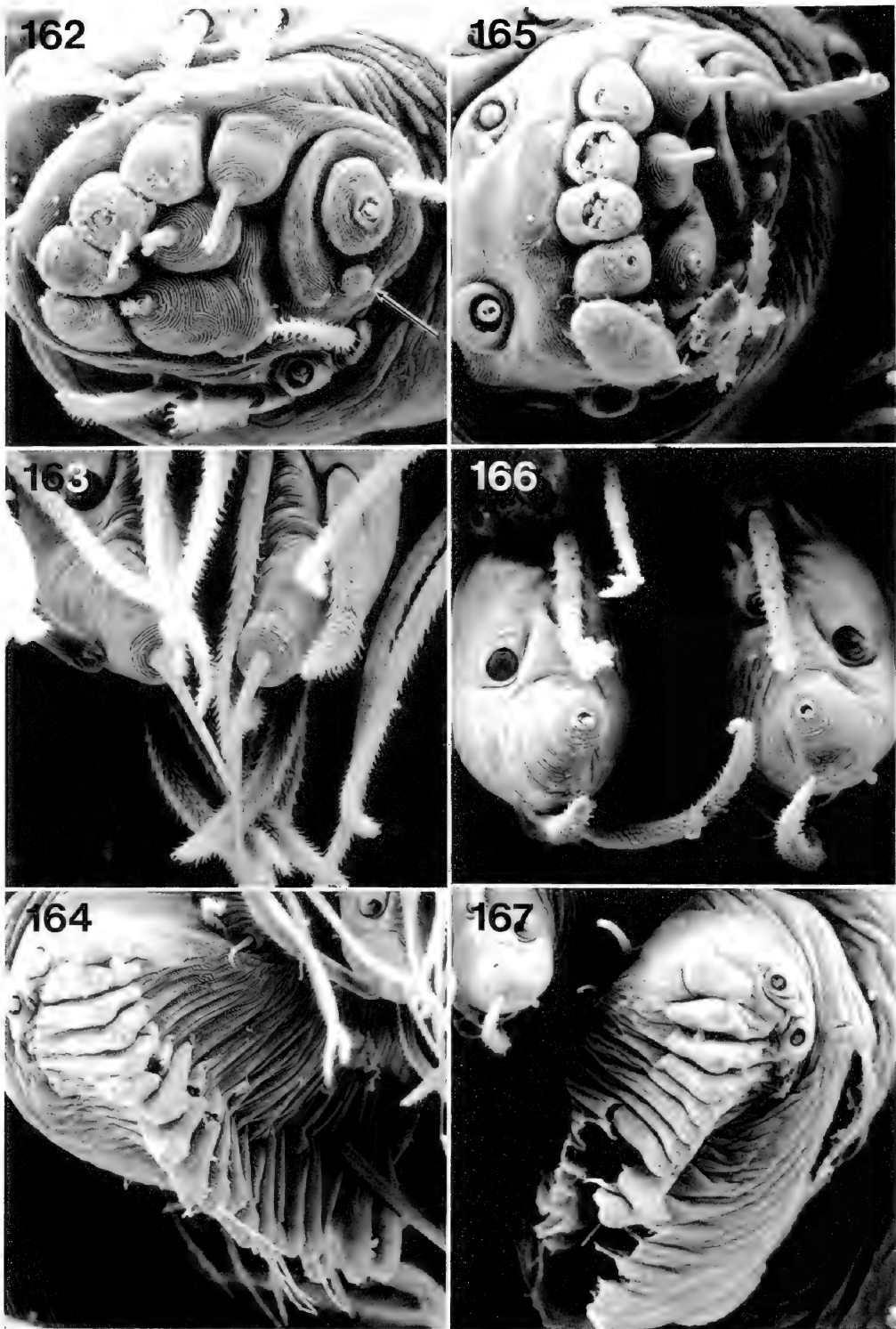
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(arrow to nubbin beneath major ampullate gland spigot), 2000×. **163, 166.** PMS, 2000×, 1790×. **164,
167.** PLS, 1000×, 1000×.
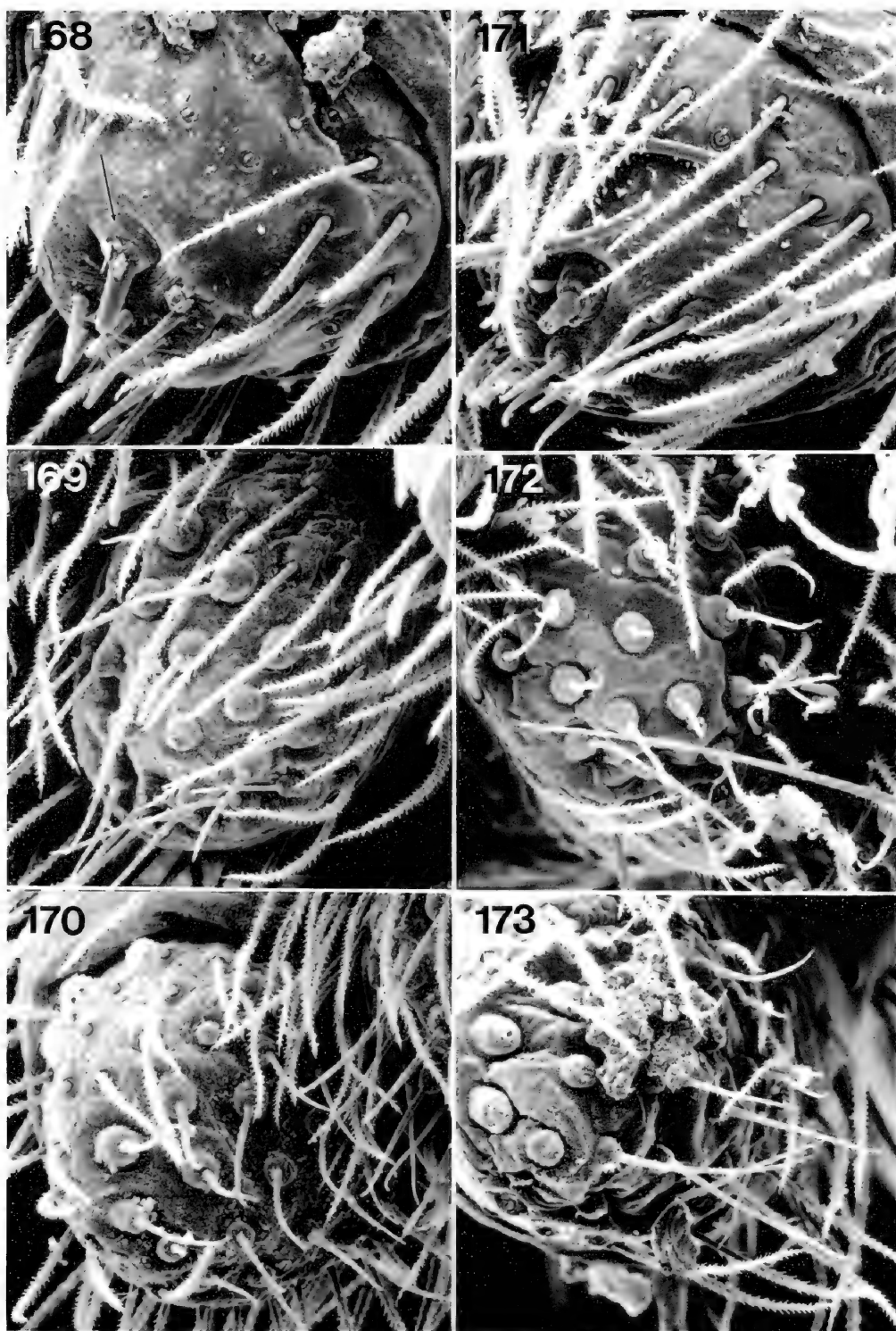
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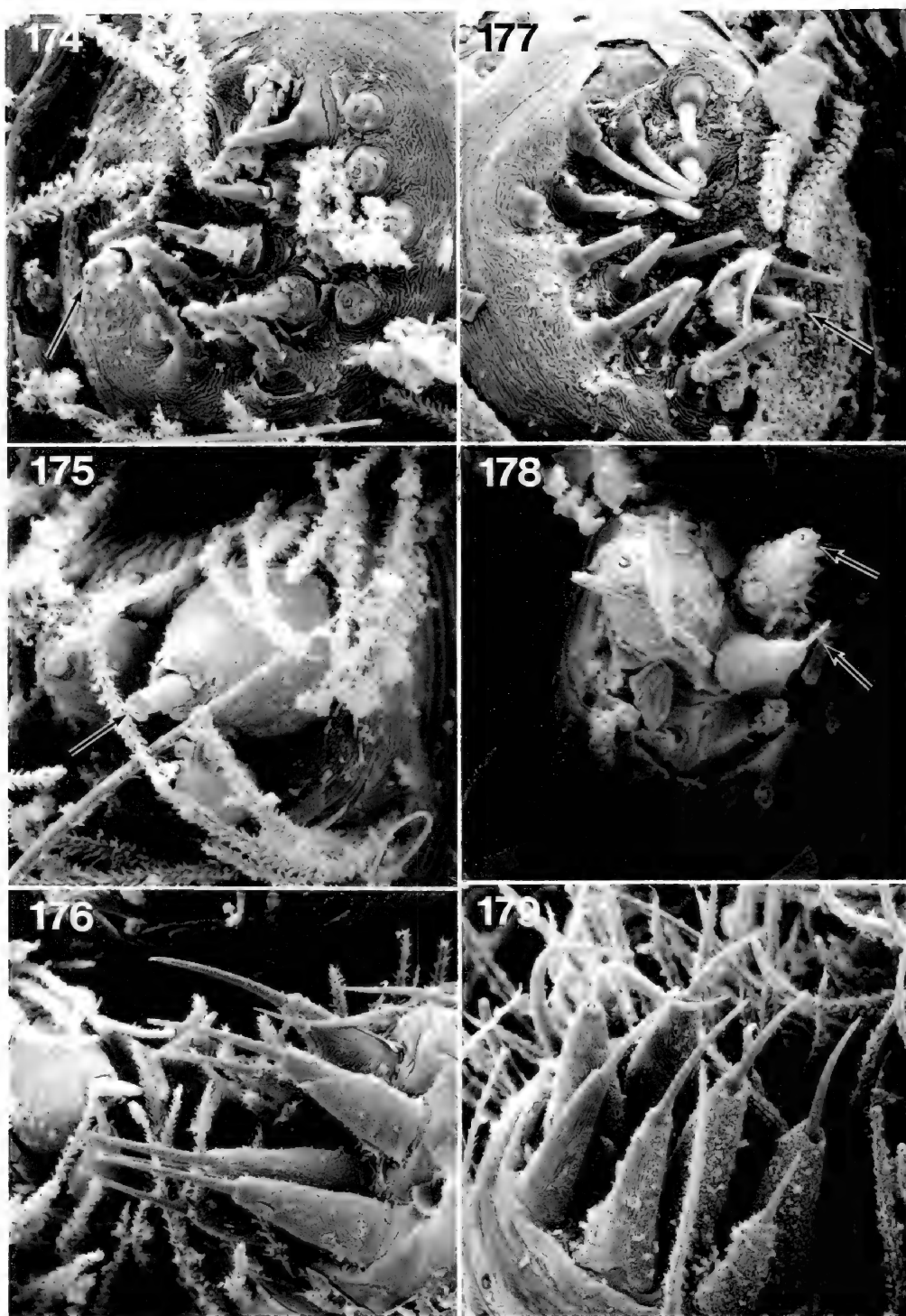
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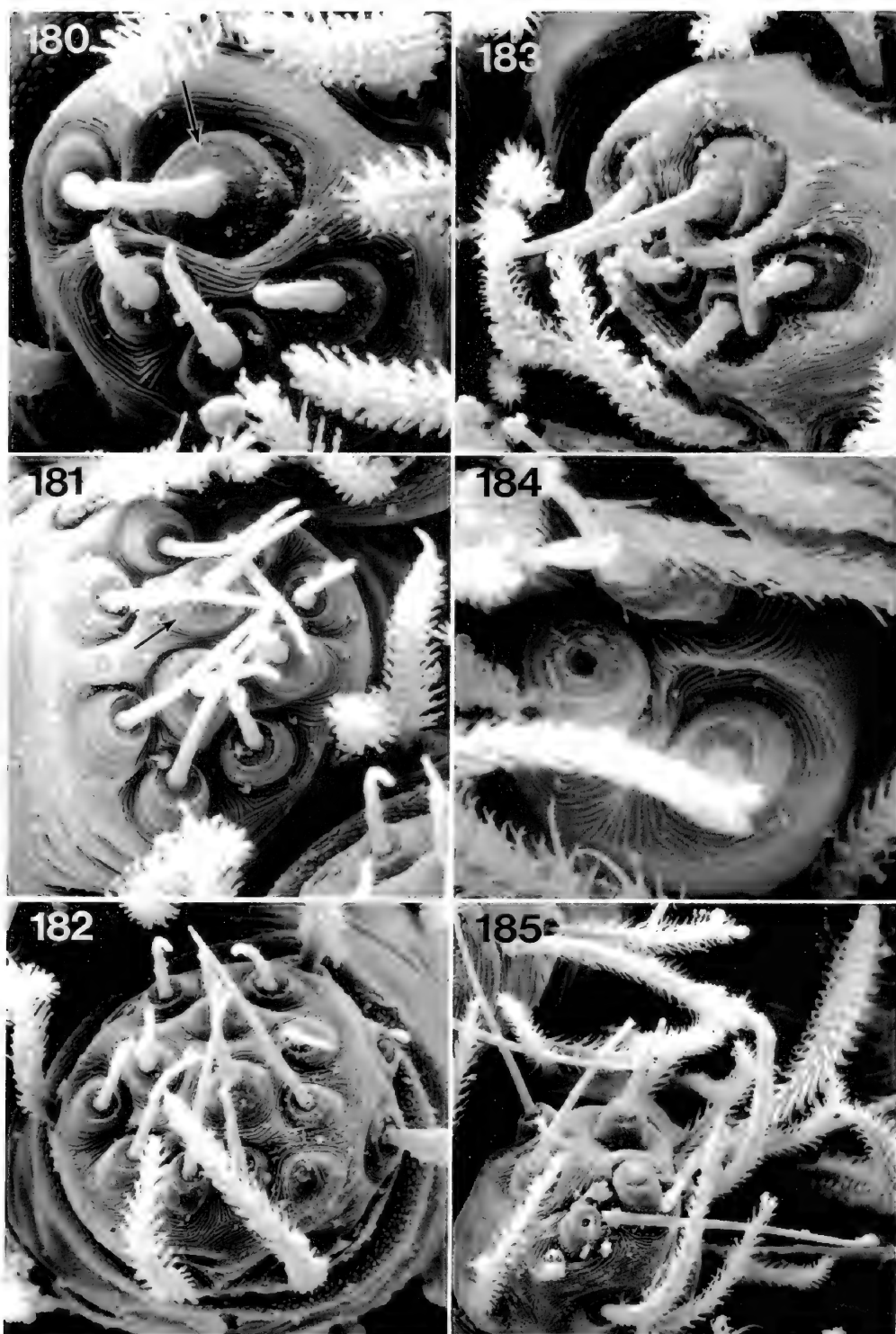
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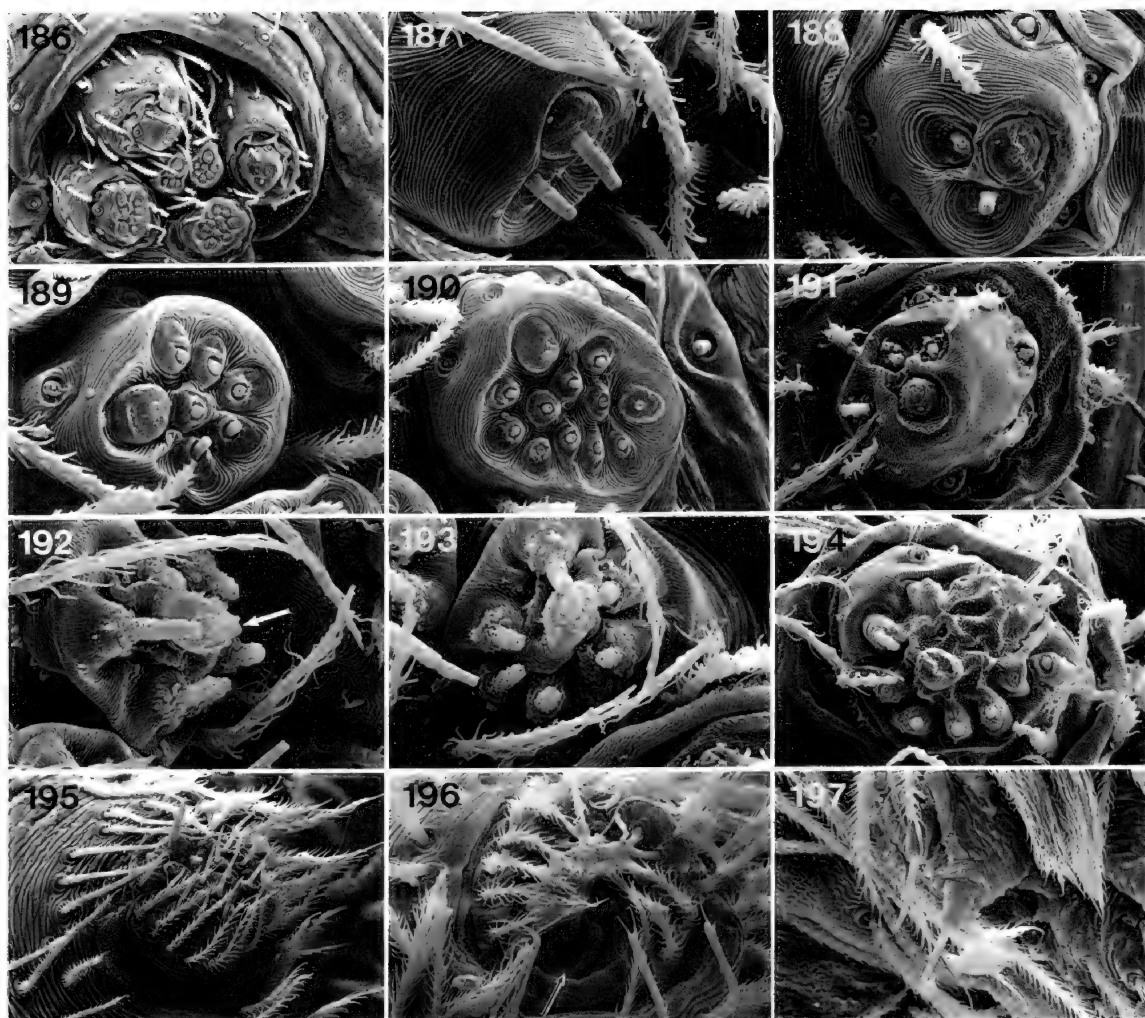
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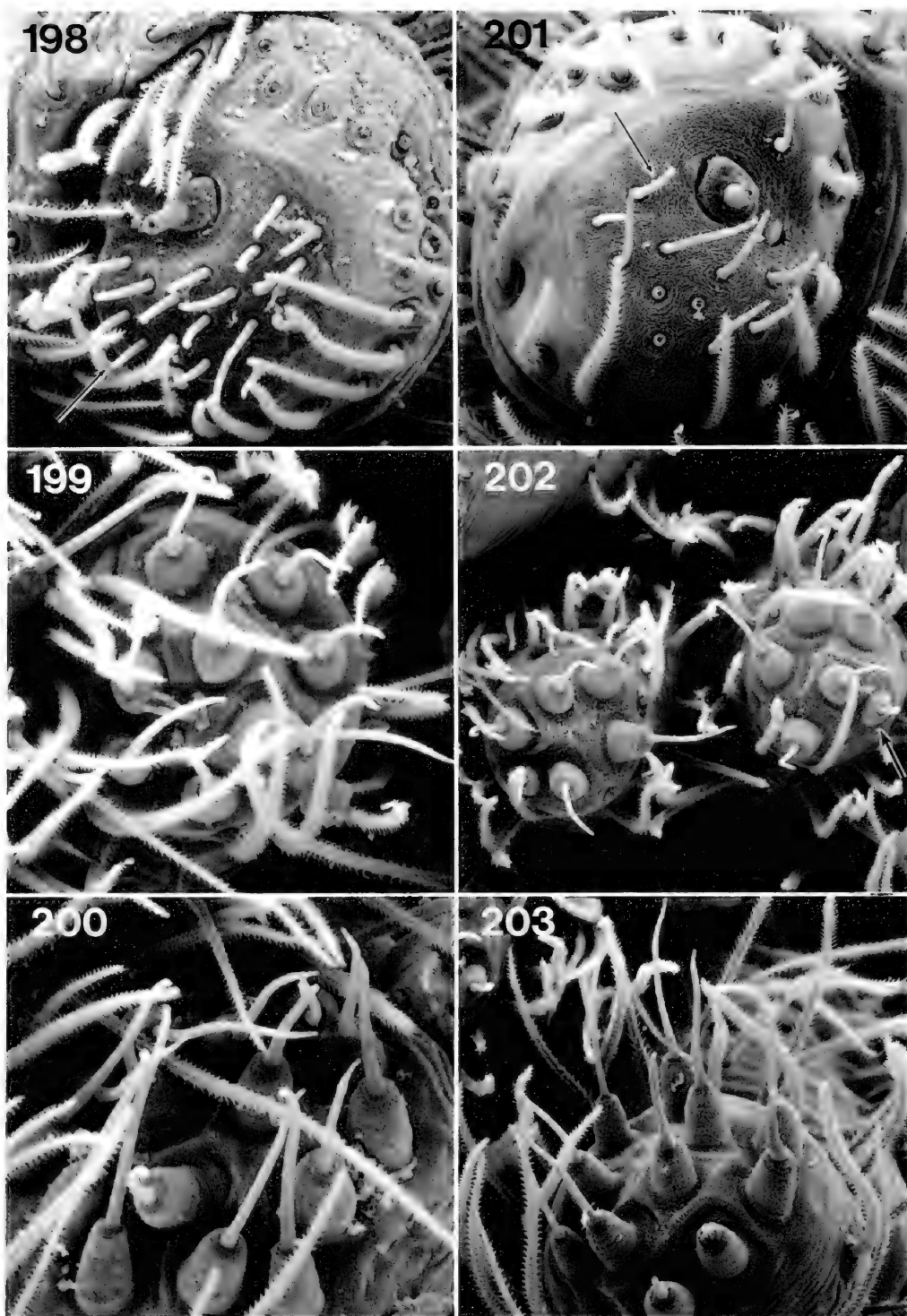
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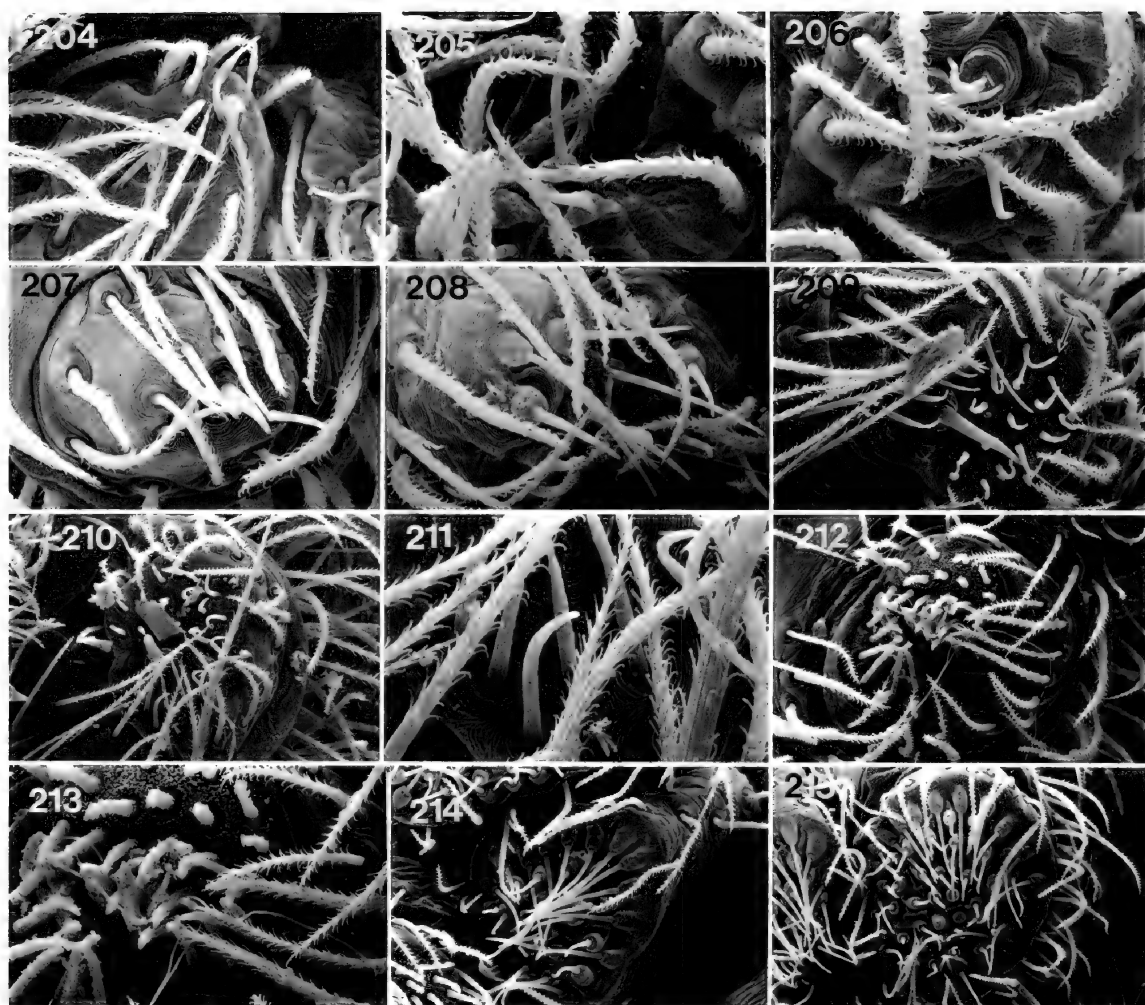
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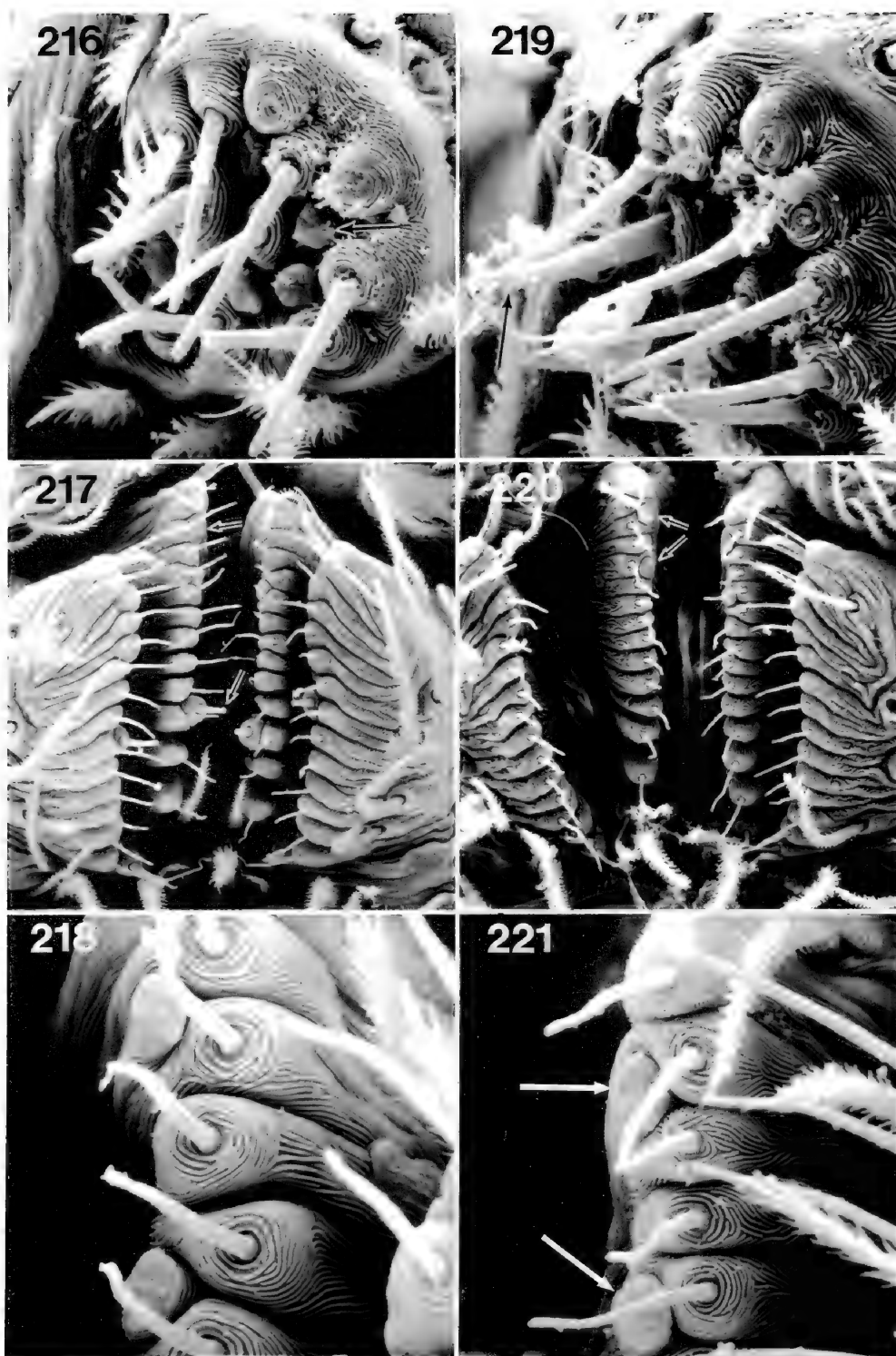
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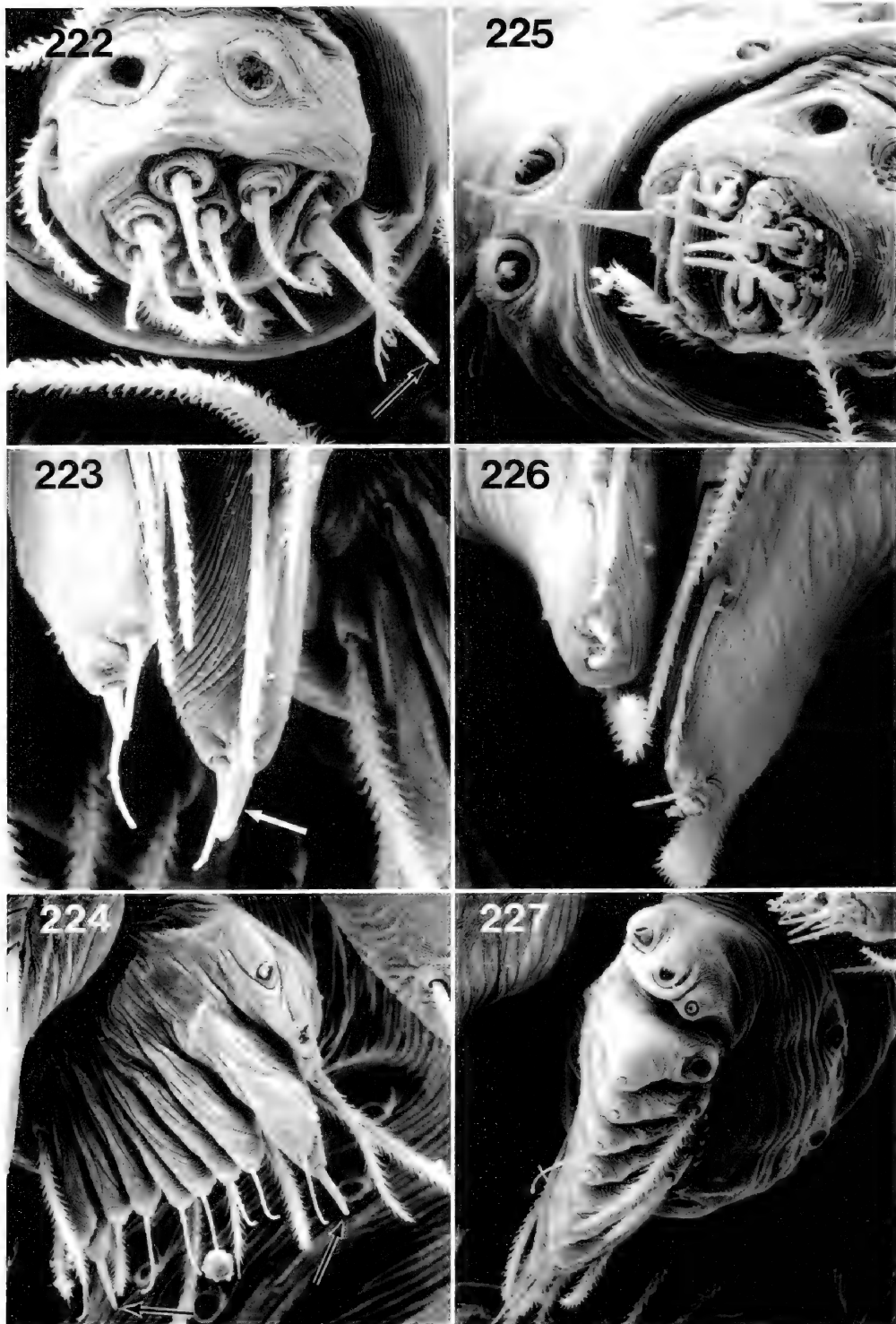
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spigot), 2000×. **224, 227.** PLS, 1000× (arrows to cylindrical gland spigots), 1125×.
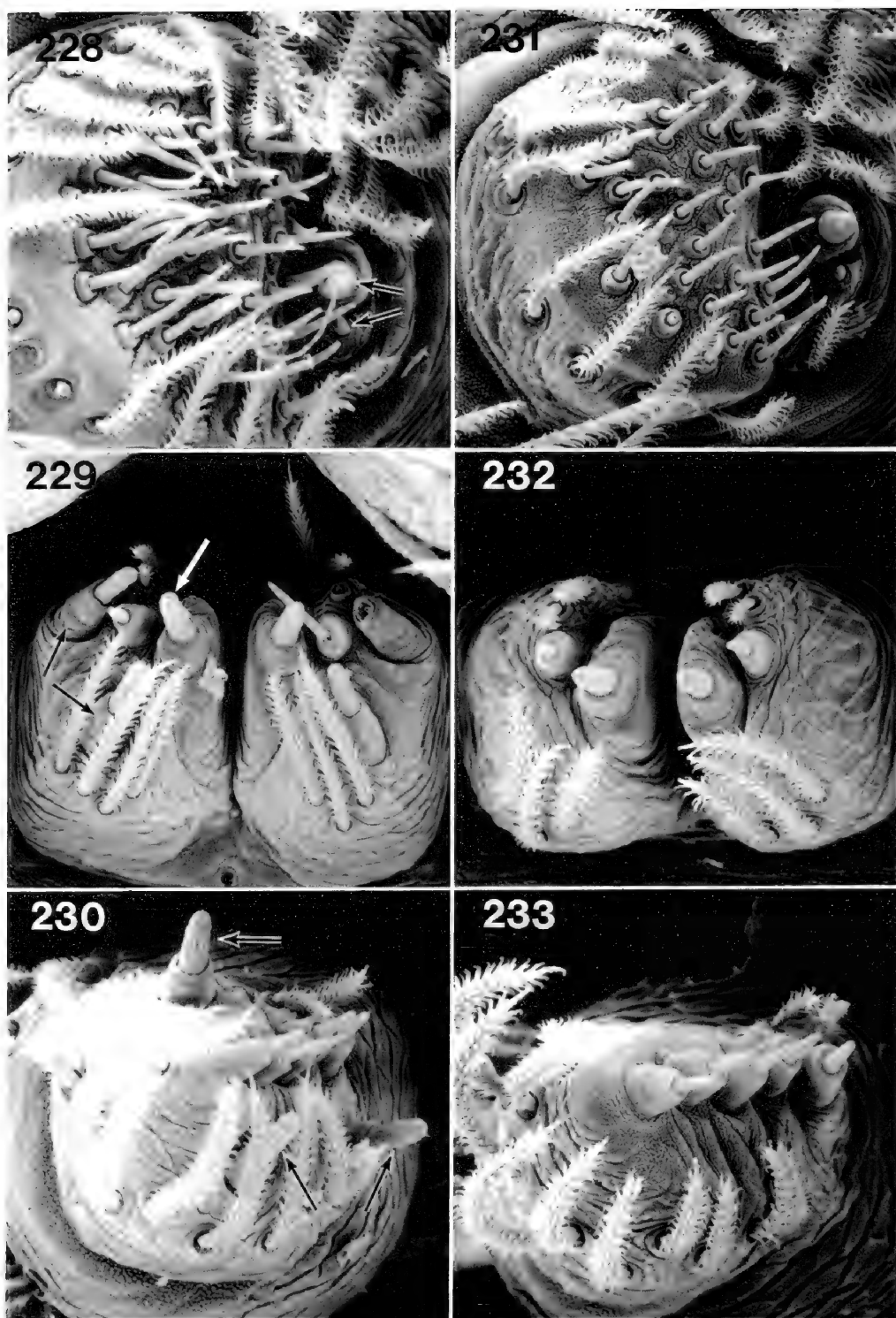
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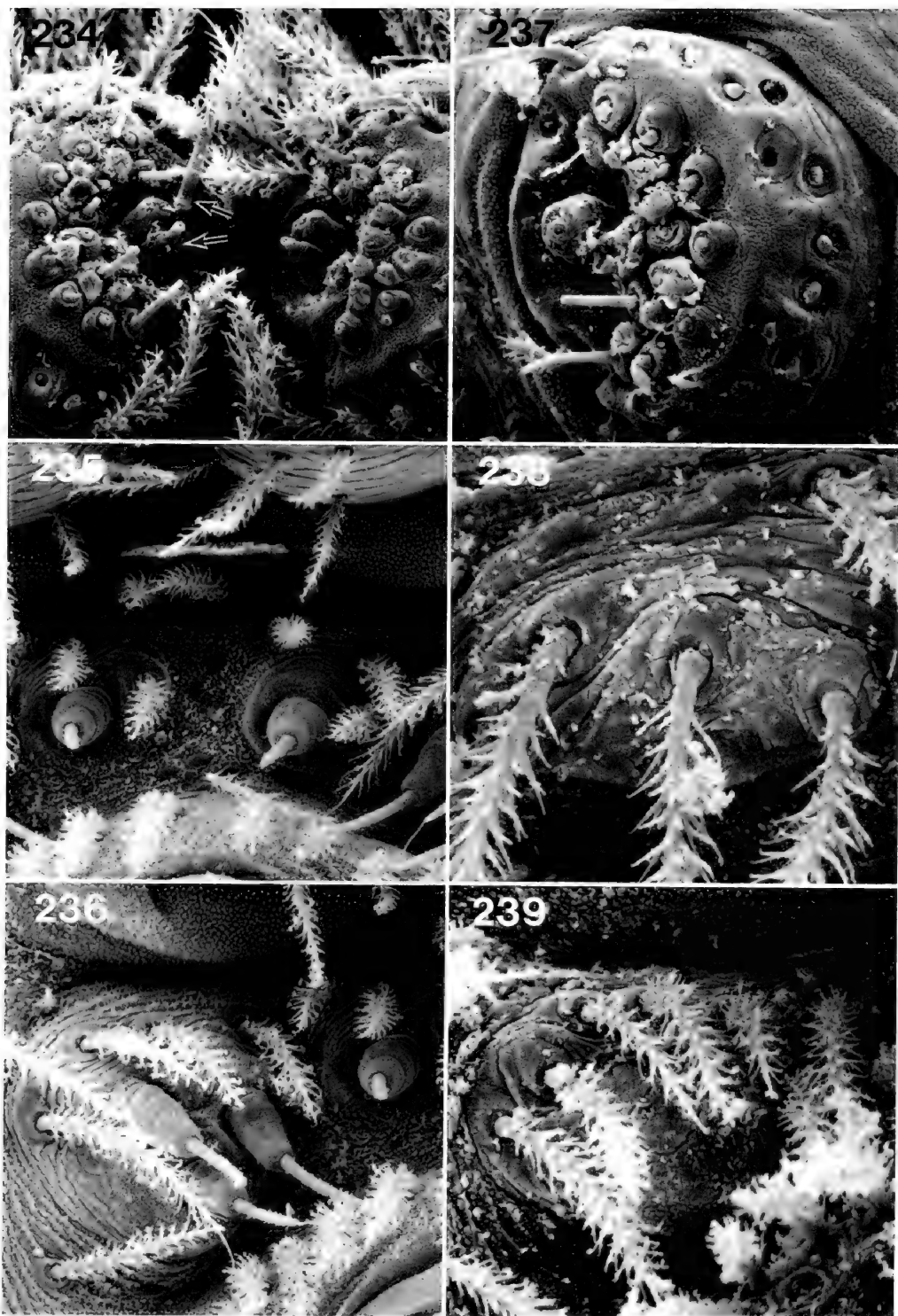
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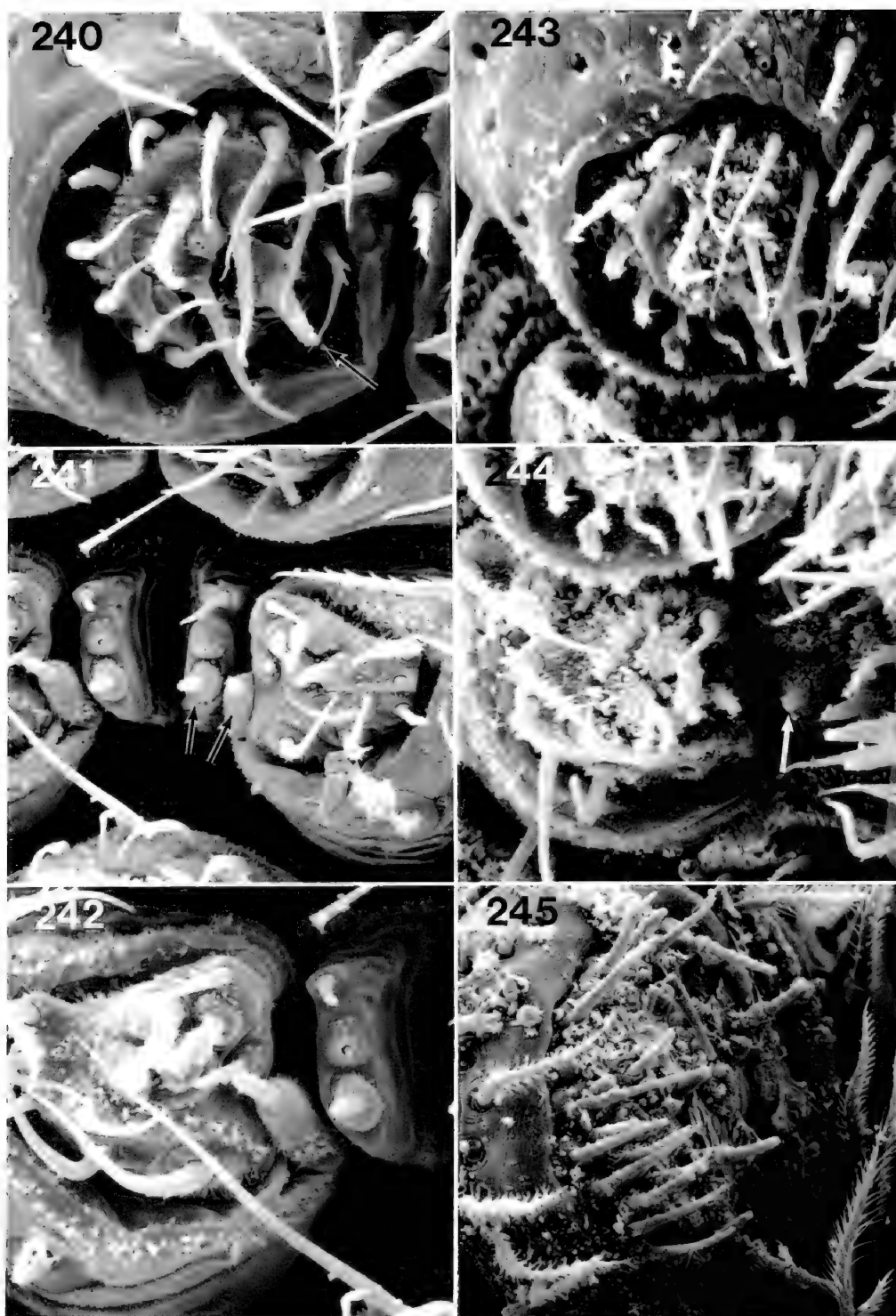
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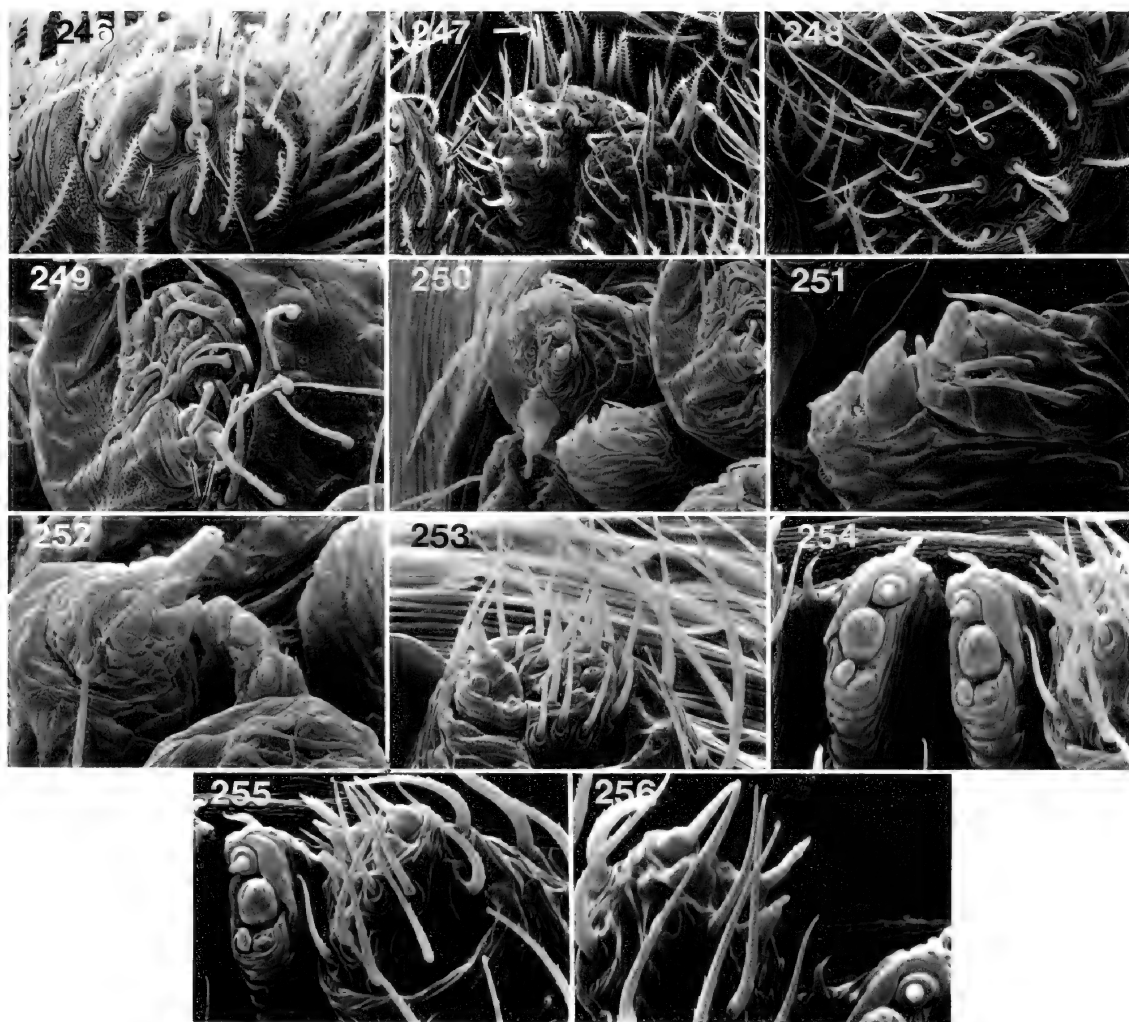
Figs. 246–256.   246–248. *Huttonia palpimanoides* O. P.-Cambridge. 249–256. *Novanapis spinipes* (Forster). 246–252. Female. 253–256. Male. **246, 249, 253.** ALS, 950× (top arrow to tartipore, bottom arrow to major ampullate gland spigot), 1750× (arrows to major ampullate gland spigot and nubbin), 1400×. **247, 251.** PMS, 550× (white arrow to minor ampullate gland spigot, black arrows to cylindrical gland spigots), 2950×. **248.** PLS, 750×. **250, 252, 254-256.** PMS and PLS, 1000×, 1550×, 2000×, 1850×, 2500×.
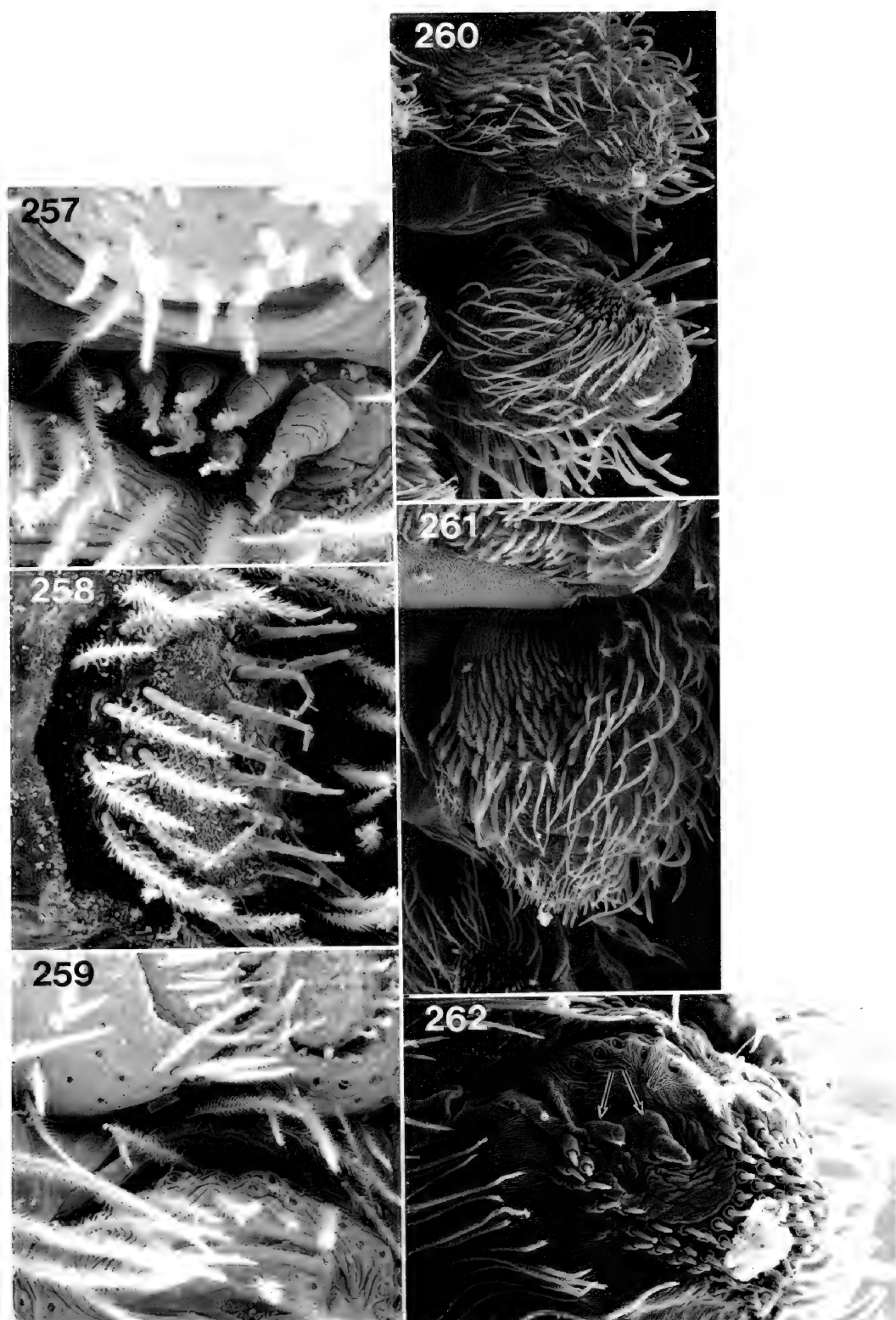
Figs. 257–262. 257–259. *Otiothops pentucus* Chickering. 260–262. *Waitkera waitakerensis* (Chamberlain). 257, 260–262. Female. 258, 259. Male. **257, 259.** PMS and PLS, 550×, 420× (reduced in females, virtually absent in males). **258.** ALS, 1000×. **260.** Left spinning field, 190×. **261, 262.** ALS, 200×, 710× (arrows to minor ampullate gland spigot and nubbin).
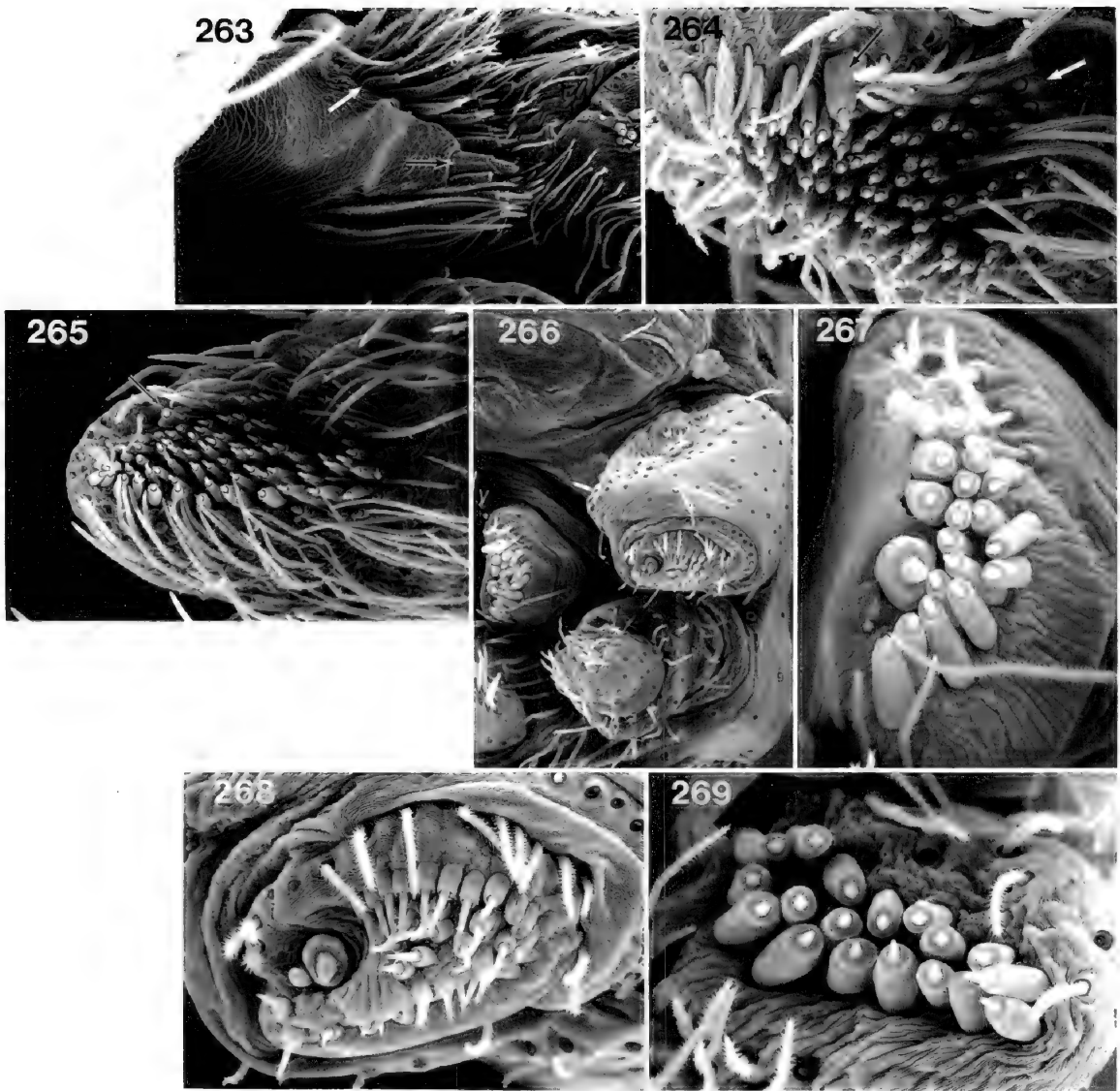
Figs. 263–269. *Waitkera waitakerensis* (Chamberlain). 263–265. Female. 266–269. Male. **263, 267.** PMS, 415× (white arrow to a paracribellar spigot, black arrow to minor ampullate gland spigot), 1125×. **264, 265, 269.** PLS, 640× (black arrow to pseudoflagelliform gland spigot, white arrow to cylindrical gland spigot), 410× (arrow to pseudoflagelliform gland spigot), 1200×. **266.** Left spinning field, 270×. **268.** ALS, 940×.
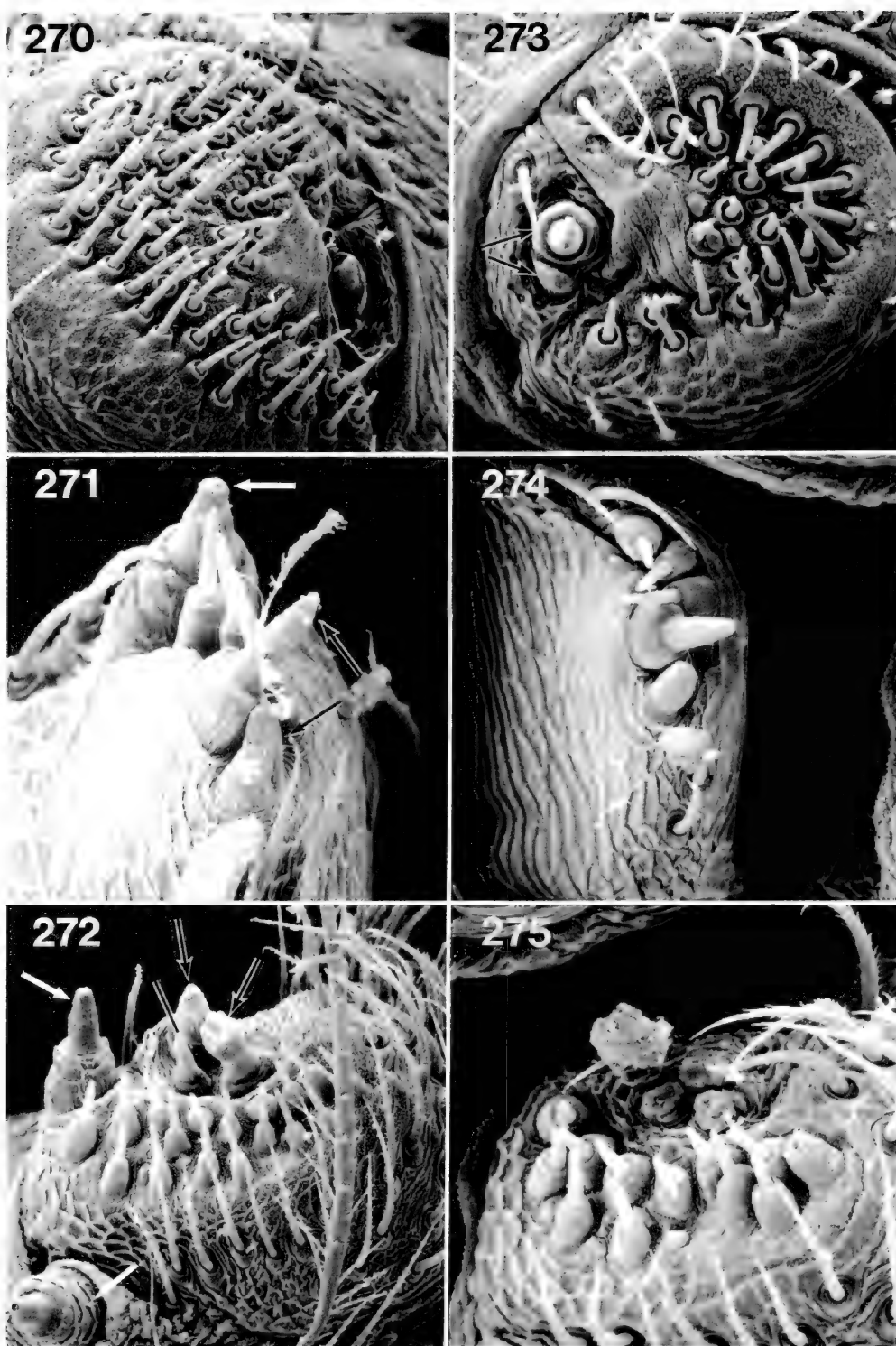
Figs. 270–275. *Tetragnatha versicolor* Walckenaer. 270–272. Female. 273–275. Male. **270, 273.** ALS, 745×, 1000× (arrows to major ampullate gland spigot and nubbin). **271, 274.** PMS, 1195× (white arrow to cylindrical gland spigot, black arrows to minor ampullate gland spigot and nubbin), 1145×. **272, 275.** PLS, 640× (black arrows to aggregate gland spigots, black line to flagelliform gland spigot, white arrows to cylindrical gland spigots), 1245×.
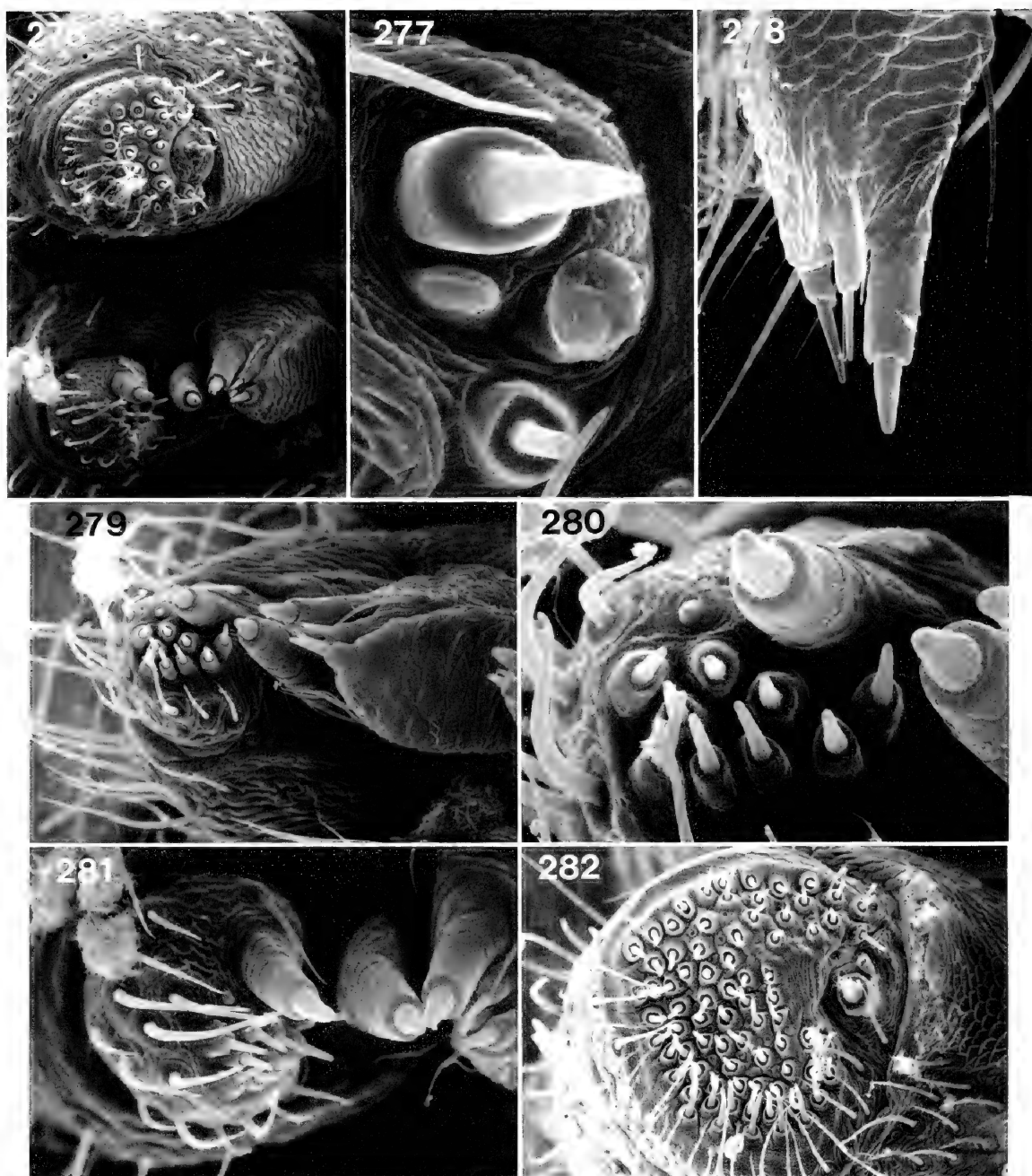
Figs. 276–282. 276–281. *Pachygnatha autumnalis* Keyserling, female. 282. *Tetragnatha versicolor* Walckenaer, female. **276.** Right spinning field, 440×. **277.** ALS major ampullate gland spigot and nubbin, 3500×. **278.** PMS, 960×. **279.** PMS and PLS, 650×. **280, 281.** PLS, 1975×, 940×. **282.** ALS, 500×.
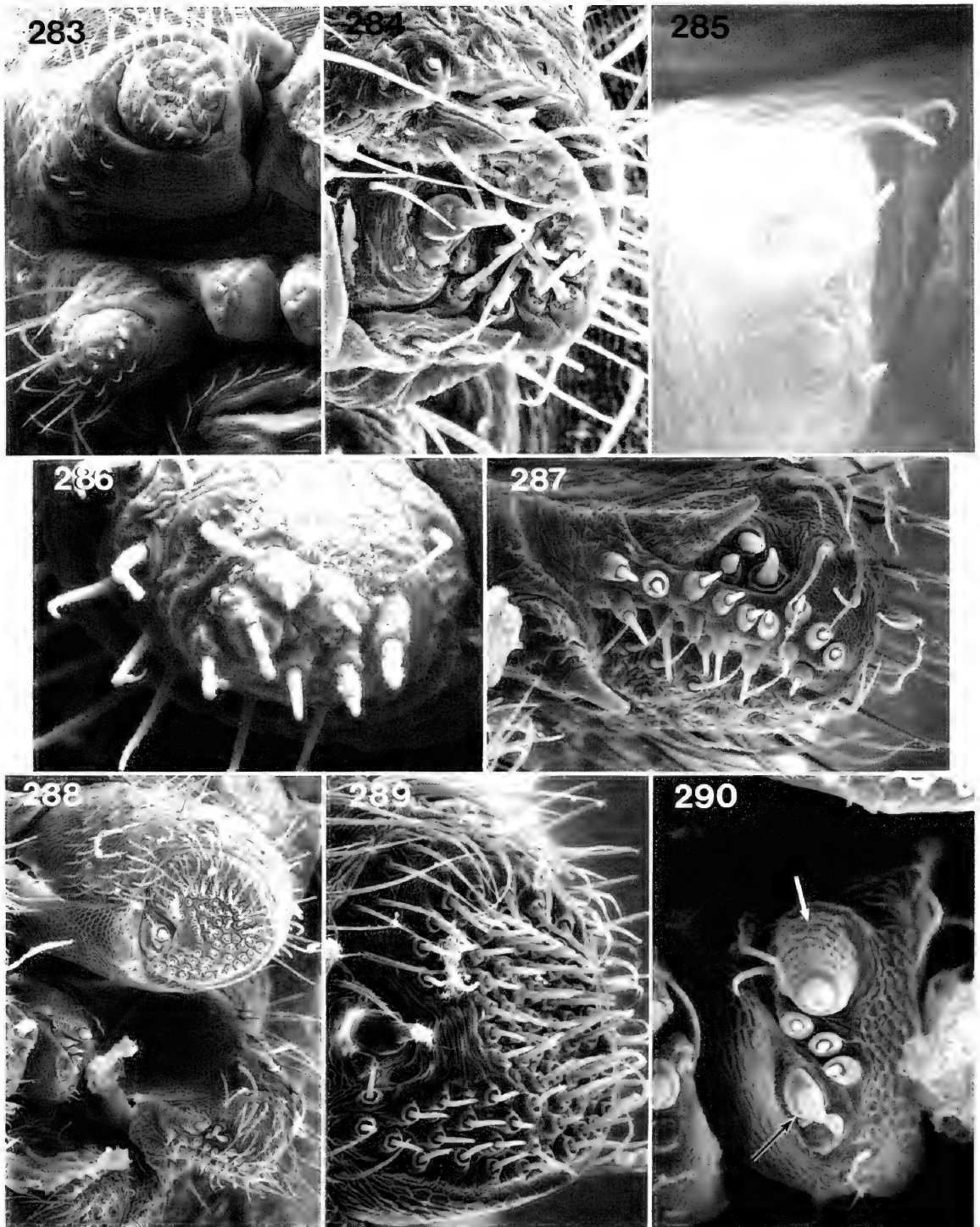
Figs. 283–290. 283–286. *Pachygnatha autumnalis* Keyserling, male. 287–290. *Tetragnatha versicolor* Walckenaer, female. **283.** Right spinning field, 410×. **284, 289.** ALS, 1075×, 610×. **285, 290.** PMS, 1950×, 660× (white arrow to cylindrical gland spigot, black arrow to minor ampullate gland spigot). **286, 287.** PLS, 1825×, 650×. **288.** Left spinning field, 210×.
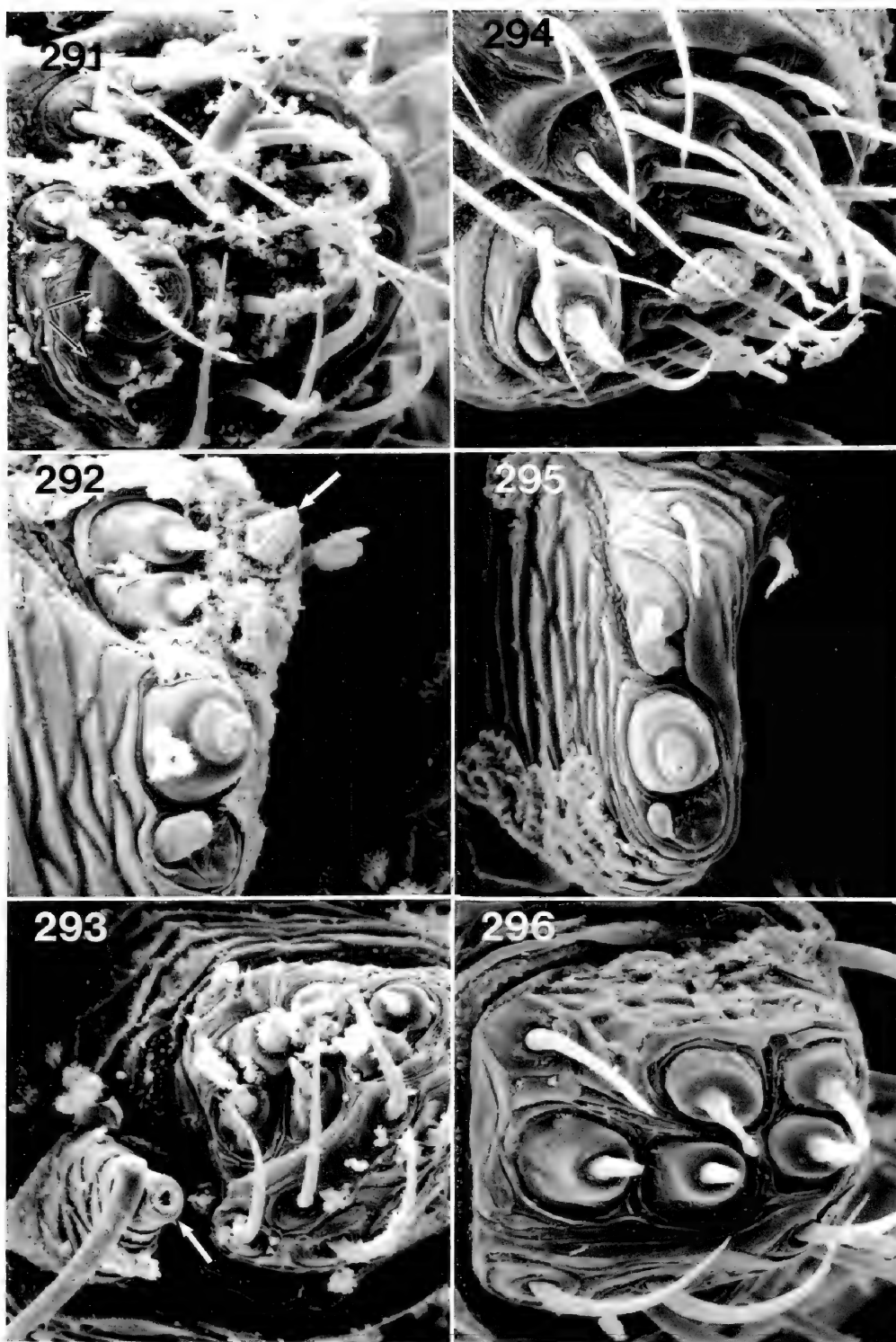
Figs. 291–296. *Crassanapis chilensis* Platnick and Forster. 291–293. Female. 294–296. Male. **291, 294.** ALS, 2410× (arrows to major ampullate gland spigot and nubbin), 2000×. **292, 295.** PMS, 3015× (arrow to cylindrical gland spigot), 2490×. **293, 296.** PLS, 2000× (arrow to cylindrical gland spigot), 2845×.
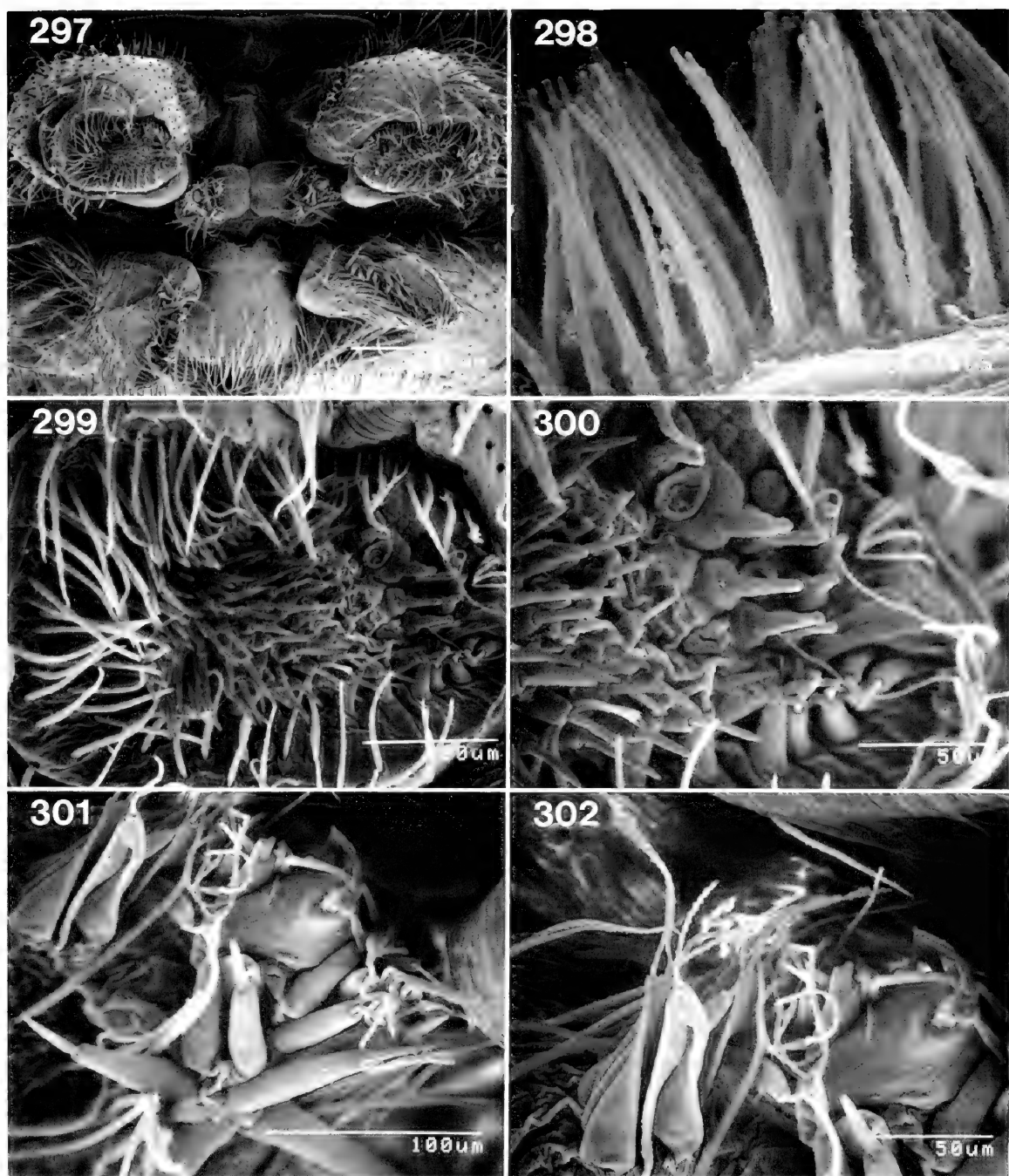
Figs. 297–302. *Macrogradungula moonya* Gray, juvenile female; micrographs by Drs. Valerie Davies and Robert Raven. **297.** Spinning field. **298.** Cribellar spigots. **299, 300.** ALS. **301, 302.** PMS.
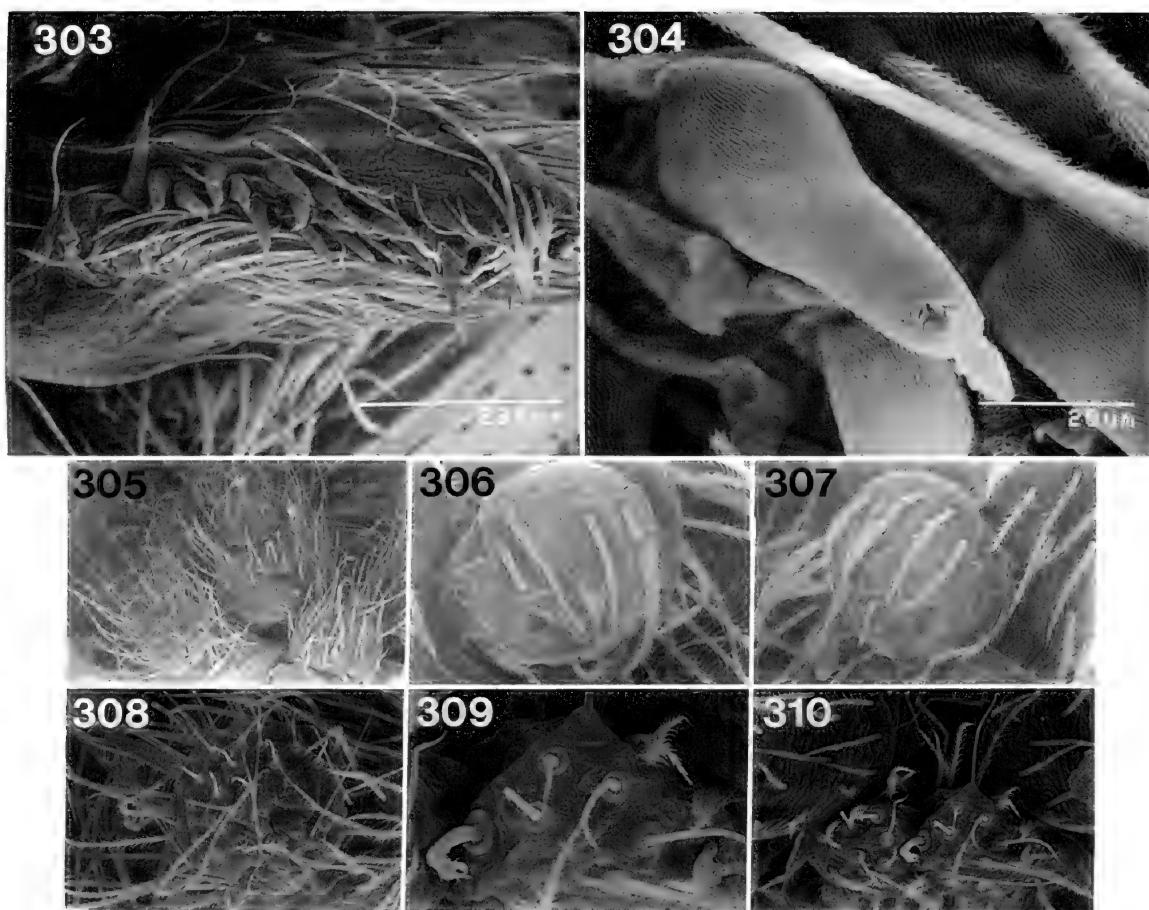
Figs. 303–310. **303, 304.** *Macrogradungula moonya* Gray, juvenile female; micrographs by Drs. Valerie Davies and Robert Raven, PMS. 305–310. *Huttonia palpimanoides* O. P.-Cambridge, male. **305.** Spinning field, 190×. **306, 307.** ALS, 750×, 700×. **308, 309.** PMS, 500×, 1150×. **310.** PLS, 480×.

tified three gland and spigot types serving the ALS. A single large "Glandula ampullacea" opens through a single large spigot situated medially; surrounding that large spigot are a group of 6–8 smaller spigots served by "tubulöse Drusen" and separated by a furrow from a large number of small spigots served by shorter, wider glands identified as "Glandulae piriformes."

Our micrographs of male and female *Hypochilus pococki* Platnick (figs. 1–12) reveal a similar organization. The cribellum is entire (fig. 7), with strobilate spigots (fig. 8). The lateral field of ALS piriform gland spigots is separated by a distinct furrow from the remaining spigots, one of which is larger than the others (figs. 1, 4, 9, 10). We consider all the spigots on the median side of the ridge to be major ampullate gland spigots, despite the size differences among them. This hypothesis is supported by the situation in females of *Ectatosticta davidi* (Simon), in which a similar furrow separates sets of piriform and major ampullate gland spigots, but none of the latter are notably enlarged (Forster et al., 1987: fig. 33).

The PMS have only a single spigot type, served by small, round to oblong glands also serving the PLS and therefore here considered as aciniforms. The PMS spigots of *H. pococki* present a range of sizes (figs. 2, 5) but minor ampullate glands seem to be absent. The same is true for female *E. davidi* (Forster et al., 1987: fig. 35).

Glatz (1972) reported two PLS spigot and gland types for *H. gertschi*, with numerous (presumably aciniform gland) spigots bearing narrow shafts (figs. 3, 6) and two most distal spigots with enlarged shafts that are served by "langen tubulösen Drüsen." Because these tubular glands are histologically similar to the tubular glands serving the ALS, they might be minor ampullate glands. However, even though minor ampullate glands are known to occur on the PLS of a few spiders (gnaphosoids and eresids; Platnick, 1990; Hajer, 1990), no cases seem to have been recorded where minor ampullate gland spigots occur on the PLS but not the PMS. It is possible, therefore, that the enlarged distal spigots represent precursors of the pseudoflagelliform and flagelliform gland spigots of orbicularians. The enlarged spigot type is clearly pres-

ent on the PLS of *H. pococki* females (figs. 11, 12), but its occurrence in *E. davidi* (Forster et al., 1987: fig. 36) is uncertain.

As Glatz (1972) noted, the morphology of all *Hypochilus* spigots (except, of course, for those on the cribellum) is similar, and unusual in that each spigot base bears several transverse and overlapping ridges, which Glatz suggested may serve to increase the mobility of the spigot. The same morphology occurs in *Ectatosticta* (Forster et al., 1987: fig. 34), but is unknown to date in any other araneomorphs.

THE FAMILY GRADUNGULIDAE

Gradungulids are of special interest because of the existence of two Australian genera, *Progradungula* and *Macrogradungula*, which still retain a cribellum; the remaining five genera have lost the cribellum and no longer build webs (Forster et al., 1987). Unfortunately, neither cribellate genus is represented by enough material in collections to allow us to present spinneret scans of adults. The spinnerets of a juvenile female *Progradungula* have been examined by Dr. M. R. Gray of the Australian Museum, who reports (in litt.) that the ALS each have six major ampullate gland spigots (of which two are slightly enlarged) grouped medially, as well as more slender piriform gland spigots, and that the PMS each have seven paracribellar spigots.

The spinnerets of a juvenile female *Macrogradungula moonya* Gray were scanned by Drs. Valerie Davies and Robert Raven of the Queensland Museum, who kindly allowed us to include those figures here (figs. 297–304). The cribellum is undivided (but posteriorly notched, fig. 297) with strobilate spigots (fig. 298). The ALS have numerous piriform gland spigots as well as about eight major ampullate gland spigots, at least one of which is conspicuously enlarged (figs. 299, 300). The PMS have about eight long aciniform gland spigots, one large minor ampullate gland spigot, and about four paracribellar spigots with expanded, sail-like bases (figs. 301, 302). The PLS have a dorsoventrally flattened tip bearing a series of about 15 elongate aciniform gland spigots and a possibly differentiated spigot, with a widened base, near the tip (figs. 303, 304).

Glatz (1972) found three ampullate glands as well as piriform glands serving the ALS in very young juveniles of *Gradungula*, but no histological work seems to have been done on the silk glands of any adult gradungulids. We present here scans for the New Zealand taxa *Gradungula sorenseni* Forster (figs. 13–18) and *Pianoa isolata* Forster (figs. 19–22).

The ALS of these species resemble those of hypochilids, having two fields of spigots, a lateral field of piriform gland spigots and a median field of major ampullate gland spigots (figs. 13, 16, 19, 20). Size differences among the latter are not pronounced.

The PMS and PLS each bear two size classes of spigots, with distinctly ridged cuticular surfaces; in each case the larger spigots are situated around the outer edges of the spinning field and surround the smaller spigots (figs. 14, 15, 17, 18, 21, 22). There are at least three possible interpretations: all the spigots may serve aciniform glands that simply fall into two size classes (with peripheral spigots enlarged to allow a level field of spigot tips arrayed on a dome-shaped spinneret); the different size classes may represent aciniform and minor ampullate gland spigots; or the larger spigots may represent paracribellar spigots that have been retained despite the loss of a functional cribellum (see below under Austrochilidae; such a retention would be unique, so far as we are aware). Until at least one gradungulid species can be examined histologically, there is little basis for choosing among these hypotheses.

THE FAMILY AUSTROCHILIDAE

Scans are presented here for representatives of both genera of the subfamily Austrochilinae, *Austrochilus melon* Platnick (figs. 27–34) and *Thaida peculiaris* Karsch (figs. 35–41). In both genera, the cribellum is entire (fig. 27); the ALS have only two major ampullate gland spigots (figs. 29, 32, 38, 39; Forster et al., 1987: fig. 111) that are separated from the piriform gland spigot field by a patch of bare cuticle (figs. 35, 38). The major ampullate gland spigot shafts are relatively smooth (fig. 39; Forster et al., 1987: fig. 112), whereas the piriform gland spigot shafts bear distinct fingerprintlike ridging (fig. 37; Forster et al., 1987: fig. 113).

The PMS of both genera have numerous small aciniform gland spigots as well as the paracribellar spigots first discovered by Peters and Kovoor (1980) in uloborids and first reported in austrochilids by Peters (1983: 246, fig. 3c, 3d). In *A. melon*, two or more paracribellar spigot shafts may originate from a common base (figs. 28, 30, 33), whereas in *T. peculiaris* only single-shafted paracribellar spigots have been detected (fig. 36; Forster et al., 1987: fig. 114). Among the aciniform gland spigots, at least in *T. peculiaris* (fig. 36) and probably in *A. melon* as well (fig. 33), is a spigot with a larger base and thicker shaft, which may serve the minor ampullate glands.

Only one PLS spigot type, presumably serving the aciniform glands, was detected in *A. melon* (figs. 31, 34), but *T. peculiaris* females have at least one distal PLS spigot that, judging by its strobilate shaft morphology, is also a paracribellar spigot (figs. 40, 41; Forster et al., 1987: fig. 115), as well as one adjacent spigot with a thick and tapering shaft (fig. 41) that may represent a pseudoflagelliform-flagelliform gland spigot precursor. Paracribellar spigots have previously been noted only from the PMS, but seem to occur on the PLS of some filistatids as well as austrochilids. The spigots on the PLS (and PMS) bear the kind of fingerprint ridging found on the ALS piriform gland spigots (figs. 36, 41).

The other subfamily of Austrochilidae, the Hickmaniinae, contains only a single species, *Hickmania troglodytes* (Higgins and Petterd). As in the austrochilines, the ALS have only two major ampullate gland spigots (figs. 42, 43, 47) plus piriform gland spigots that vary in size, with the more medially situated spigots having smaller bases and shafts than those situated near the periphery of the spinning field (figs. 42, 47). The PMS are equipped with several aciniform gland spigots, paracribellar spigots (apparently with only one shaft per base), and one enlarged spigot that may serve the minor ampullate glands (figs. 44, 45, 48, 49). The PLS have numerous aciniform gland spigots of varying sizes (figs. 46, 50), with the largest spigots occurring basally; no paracribellar spigots were detected.

THE FAMILY FILISTATIDAE

The silk glands of the Mediterranean species *Filistata insidiatrix* (Forskal) have been

studied in detail by Glatz (1972) and Hajer (1990); we present here scans of females of the American species *Kukulcania hibernalis* (Hentz) (figs. 51–61) as well as both sexes of *F. insidiatrix* (figs. 62–72). Unlike the hypochiloids and austrochiloids, the filistatid cribellum is divided (fig. 51) and bears claviform rather than strobilate spigots (fig. 52).

Glatz (1972) reported that the ALS of *F. insidiatrix* have three ampullate glands as well as numerous piriform glands. As in *Hypochilus*, one of the ampullate glands is longer than the other two; the longer one serves the large major ampullate gland spigot that is set off from the piriform field by bare cuticle. Hajer (1990: table 1; note that the headings for the ALS and PLS are reversed) reported only two ampullate glands in adult males and females of the same species. Our results agree with those of Glatz rather than Hajer; scans of both *F. insidiatrix* and *K. hibernalis* show three major ampullate gland spigots (figs. 54, 55, 63, 64, 68), with the second spigot adjacent to the large one and the third one included within the field of piriform gland spigots. Our examination of a juvenile of *F. insidiatrix* indicates that a third major ampullate gland spigot is probably present even in that stage, but is small and easily overlooked because it is surrounded by piriform gland spigots. So far as we are aware, a configuration of three major ampullate gland spigots has not yet been found in any other spiders.

Also notable on the ALS of these filistatids is a row of strong, specialized setae situated on the proximal segment (figs. 53, 54, 62, 67); Hajer (1990: 403) indicated that "the secretion wiped with calamistrum off the spinning area of cribellum is drawn over the hairs along their surface."

Both Glatz and Hajer reported four gland types serving the PMS of *F. insidiatrix*, which Hajer identified as two size classes of aciniforms, plus one (minor) ampullate gland and one tubuliform (= cylindrical) gland. There are difficulties with this interpretation, however. Hajer's "tubuliform" gland was found by him in juveniles and adults of both sexes. In other spiders, these glands produce silk that is used in egg case construction, and do not occur in males (Kovoor, 1977a, 1987; Coddington, 1989). Because each of the gland

types of filistatids occur in both sexes, it seems unlikely that any of them are homologous with the cylindrical glands of "higher" araneomorphs.

Our scans of *K. hibernalis* females reveal a total of 11 PMS spigots (figs. 56–59); Glatz and Hajer reported eight and seven spigots, respectively, in *F. insidiatrix*, and the male of that species we scanned appears to have seven (fig. 69). Most noticeable in both species are three large spigots bearing widened, transversely ridged, and apparently flexible shafts (figs. 56–58, 65, 69); in *K. hibernalis*, two of the three are flared below the tip. Hajer (1990: 405) found that:

> The three external spigots at the front side are very similar, they have long terminal parts. Two of them are attached to identical spherical acinose glands, containing epithelium with acidophilic secretion. The third spigot is connected to an elongated gland containing epithelium with basophilic secretion. It is consequently the acidopholic epithelium that is absent in this case. The first two glands can be classified as gl. aciniformes, the third one as gl. tubuliformes.

We suggest that some or all of these three spigots may serve paracribellar glands, which were not recognized at the time of Glatz (1972) and were not considered by Hajer. This hypothesis may explain Hajer's observation (1990: 401) that "The glandulae aciniformes in *F. insidiatrix* are very diverse." Two spigots that are similar to the narrower of these three PMS spigots occur distally on the PLS (figs. 60, 61, 66, 70, 72). Hajer thought these PLS spigots serve cylindrical glands, but again he found those glands in juveniles as well as adults of both sexes (1990: table 1, but cf. p. 412). Because the three PMS spigots are so derived in shaft morphology, their homology with the paracribellar spigots of other cribellates could be questioned. However, if they are modified paracribellar spigots, and if (as in *Thaida*) filistatids once had normal paracribellar spigots on the PLS as well as the PMS, then the modification of the PMS paracribellar spigots should have affected the PLS spigots as well. Because the PLS spigots in question do show the same modification, the hypothesis is not refuted.

Of the other PMS spigots in *K. hibernalis* (figs. 57, 58, 69, 71), one has a greatly enlarged base and wide shaft, and was identified

as serving the (minor) ampullate gland in both histological studies of *F. insidiatrix*. The remaining spigots of *K. hibernalis* include a row of six small shafts and one longer but narrow spigot originating on the opposite side of the group of three large spigots; at least the former serve the aciniform glands, and the latter may serve an enlarged aciniform gland as well. The PLS (figs. 60, 61, 66, 70) bear numerous small spigots, again serving aciniform glands, as well as the two larger spigots mentioned above. One double-shafted spigot (fig. 60) may be teratological.

THE FAMILIES SCYTODIDAE, SICARIIDAE, DRYMUSIDAE, AND LOXOSCELIDAE

Millot (1930) considered the silk spinning apparatus of *Scytodes thoracica* (Latreille) highly reduced, and showing individual variation in the degree of atrophy, especially of those glands serving the PMS. Our scans of *Scytodes* sp., from Texas, show a similarly reduced array of spigots (figs. 73–76), and agree with Millot's results in showing no significant sexual differences. The ALS bear a single, relatively wide major ampullate gland spigot and numerous smaller piriform gland spigots (figs. 73, 75). In both sexes, the PMS and PLS each bear a single spigot (figs. 74, 76), presumably serving the aciniform glands. There is a small group of spicules on the inner margin of the PMS (fig. 74). The colulus is relatively large, and the posterior spinneret pairs are closely spaced, with the flattened lateral edge of the tetrahedral PMS fitting against the flattened median edge of the PLS.

The spigots of *Sicarius* (figs. 77–82) are difficult to scan, as the spinnerets are extremely hairy, and attempts to remove the hairs almost invariably result in breakage of the spigot shafts as well. Millot (1930) found about 80 small glands, all very similar. Our scans do not allow any major ampullate gland spigots to be resolved with certainty among the numerous piriform gland spigots on the ALS, but one spigot with a straighter shaft may serve the major ampullate gland (fig. 80; cf. fig. 77). There seems to be only a single spigot type (presumably serving the aciniform glands) on the PMS (with four such spigots) and PLS (with multiple spigots) of both sexes (figs. 78, 79, 81, 82).

The silk glands of *Drymusa* sp. have apparently not been studied. Their ALS have a single, relatively small major ampullate gland spigot, with perhaps a nubbin of a second represented in females (fig. 83; cf. fig. 86). Among the numerous piriform gland spigots, those situated laterally are larger and bear longer shafts than those situated more medially. The tetrahedral PMS bear a single (presumably aciniform gland) spigot in both sexes (figs. 84, 87), and similar spigots occur on the PLS, with fewer in males than in females (figs. 85, 88). A large field of spicules, similar to those of *Scytodes*, occurs on the inner margin of the PMS (fig. 87).

Millot's (1930) studies of *Loxosceles distincta* (Lucas) yielded results concordant with our scans of *Loxosceles reclusa* Gertsch and Mulaik (figs. 89–95), *Loxosceles laeta* (Nicolet) (fig. 96), and *Loxosceles rufescens* (Dufour) (figs. 97–102). The single major ampullate gland spigot on the ALS is greatly widened in both sexes, with its shaft transversely ridged basally and longitudinally ridged apically (figs. 89, 93, 97, 98). The piriform gland spigots have relatively long shafts (figs. 89, 93). The tetrahedral PMS are devoid of spigots in both sexes (figs. 90, 94, 99, 101). Females have several (presumably aciniform gland) spigots on the PLS (figs. 91, 96, 100), but (as noted by Millot) these may be lacking in males (fig. 95; note that *L. rufescens* males retain one PLS aciniform gland spigot, figs. 101, 102). In both sexes, the PLS tip bears a row of highly modified setae (figs. 91, 92, 100, 102); in females, they are situated in a slight depression that could conceivably be homologous to the deep pit found in plectreurids (see below).

THE FAMILY DIGUETIDAE

As currently limited (Brignoli, 1983; Platnick, 1989a), this family contains three genera, one of which (*Pertica*) is known only from a single female type specimen. We present here spinneret scans for the other two genera, *Diguetia* (figs. 103–111) and *Segestrioides* (figs. 112–120); the silk glands of *Diguetia canities* (McCook) were studied by Lopez (1984).

In *Diguetia* sp., the ALS of both sexes bear only two spigots, one of which is considerably widened (figs. 103, 107). Comparison with

Segestrioides (see below) suggests that both these spigots serve the major ampullate glands, and that the piriform gland spigots have been lost in this genus. Lopez (1984) identified two categories of glands serving the ALS; his "Category B glands" seem to be major ampullates but his "Category A glands" were not identified as piriforms or any other standard gland type.

The PMS and PLS of *Diguetia* seem to be subject to variation (possibly at the species level as well as between sexes). The examined females have three spigots on the PMS (fig. 104). Two are relatively large and may serve the minor ampullate glands; the third seems similar in morphology to the numerous small spigots found on the PLS (fig. 106), which therefore probably serve the aciniform glands (note, however, that Lopez, 1984, identified only one gland type serving the PMS). Some (but not all) males examined have apparently lost the small spigot on the PMS (fig. 108), and those males also have no spigots on the PLS (fig. 109) and would seem to have lost their aciniform glands. Those males that retain a small PMS spigot (fig. 110) also retain at least a few aciniform gland spigots on the PLS (fig. 111). The PMS are tetrahedral (as in *Scytodes*, *Loxosceles*, and *Drymusa*), but the spigot bases are fused to from a distal ring (figs. 104, 108). Also notable on the PMS are a group of two or three anteromedially situated, thickened setae originating from distinctive bases with elevated rims (figs. 104, 105). Similar setae occur in the other diguetids and plectreurids discussed below (figs. 113, 116, 125, 128, 131), but apparently not in the other taxa examined. Some of those taxa, such as *Scytodes* sp. and *Drymusa* sp. (figs. 74, 76, 84, 87), have a single large seta in a similar position, but that seta seems not to have the peculiar base of the modified diguetid and plectreurid setae.

In both sexes of the Chilean species *Segestrioides tofo* Platnick, the two ALS major ampullate gland spigots appear similar to those of *Diguetia* (figs. 112, 115), but the piriform gland spigots remain, and are oddly modified, with several having greatly widened shafts similar to those of pholcids (see below). The same seems to be true for females of the Peruvian species *Segestrioides bicolor* Keyserling (fig. 118).

The PMS and PLS of *Segestrioides* are similar to those of *Diguetia*. Females have two large and one small spigots on the PMS (figs. 113, 119), and a single (relatively large) spigot on the PLS (figs. 114, 120). Males may lose the smaller PMS spigot as well as the single PLS one (figs. 116, 117). The PMS are tetrahedral and the fused spigot bases form a distal ring (figs. 113, 116, 119); modified setae with elevated bases are found around the anteromedian edge of the PMS (figs. 113, 116).

THE FAMILY PLECTREURIDAE

The two known genera of plectreurids (*Plectreurys* and *Kibramoa*), from southwestern North America and Cuba, have bizarre spinnerets (figs. 121–132); unfortunately no histological or histochemical work seems to have been done on their silk glands.

In both sexes of *Plectreurys tristis* Simon, the ALS bear only two spigots (figs. 121, 124). Again, comparison with the confamilial genus *Kibramoa* indicates that both these spigots probably serve the major ampullate glands, and that the piriform gland spigots have been lost in *Plectreurys* (just as in *Diguetia*). Here again, the more posteriorly situated of the major ampullate gland spigots is enlarged. The most striking modification of the ALS in *Plectreurys*, however, is the prolongation of the anteromedian edge of the spinneret tip into a distinct hook (figs. 121, 124). The same structure exists in both sexes of *Kibramoa suprenans* (Chamberlin), where the hook has a somewhat sharper tip (figs. 127, 130). How the hook functions in silk manipulation is unknown.

The PMS of both male and female *P. tristis* are tetrahedral, bearing two spigots, similar in size and shape and with their bases fused to form a distal ring (figs. 122, 125), whereas the PLS of both sexes are apparently devoid of spigots. The PMS spigots could thus serve either minor ampullate or aciniform glands, but comparison with diguetids suggests that the former hypothesis is the more likely. Here again, the PLS are most notable for a different sort of modification altogether. In both sexes, the tip of those spinnerets houses a deep depression, bordered by an oval rim (figs. 123, 126); a row of highly fringed setae originate

from the bottom of the depression. The same PLS setal pit occurs in *K. suprenans* (figs. 129, 132).

The ALS of *K. suprenans* again bear two major ampullate gland spigots. As in the diguetids, the more anteriorly situated spigot is narrower and obliquely set relative to the widened, more posteriorly situated spigot. Both sexes of *K. suprenans*, however, retain a few small (and possibly nonfunctional) piriform gland spigots (figs. 127, 130). The PMS and PLS do not depart significantly from those of *P. tristis*; the PMS are tetrahedral with fused spigot bases forming a distal ring, and the thickened, anteromedially situated setae with rimmed bases are conspicuous (figs. 128, 131).

THE FAMILY PHOLCIDAE

Pholcid silk glands have been studied by Apstein (1889), Millot (1926, 1929, 1931a), Hopfmann (1935), and Kovoor (1986). The gland shapes and duct pathways are extremely complex, and Millot (1929) argued that the gland shapes do not accord well with Apstein's (1889) standard classification of gland types based on shape. Subsequently, he summed up his studies of three genera (*Pholcus*, *Holocnemus*, and *Spermophora*) by indicating that they have a relatively uniform arrangement including two gland types, a pair of anterior glands opening on the PMS and a pair of huge glands opening on the ALS, that are "formations sans analogues, chez les autres Araignées" (Millot, 1931a: 82).

The ALS of *Pholcus phalangioides* (Fuesslin) are marked by an enormously enlarged and widened spigot (figs. 133, 136) identified by Hopfmann (1935) and Kovoor (1986) as serving a highly modified piriform gland (Millot's "glandes B"). Next to the enlarged spigot is a much smaller one, with a sharply pointed shaft, identified by Kovoor (1986) as serving the (major) ampullate glands (Millot's "glandes C"). The remaining, smaller spigots are widened (although not so strongly as the largest spigot) and would thus seem also to serve modified piriform glands (Millot's "petites glandes").

The PMS are tetrahedral, bearing two spigots with their bases fused into a distal ring (figs. 134, 137). The larger, more anteriorly situated spigot was identified by Kovoor (1986) as serving the (minor) ampullate glands; the smaller spigot serves Millot's "glandes K," which are presumably modified aciniform glands. The PLS are devoid of spigots in both sexes (figs. 135, 138).

THE FAMILY TETRABLEMMIDAE

Scans of the American species *Caraimatta sbordonii* (Brignoli) (figs. 139–144) and an unidentified species from Singapore (figs. 23–26) show a similar pattern of spigots. The ALS seem to have two major ampullate gland spigots as well as a relatively small number of piriform gland spigots (figs. 23, 139, 142); some of the piriform gland spigots of *C. sbordonii* seem to be slightly widened. The PMS have one relatively large spigot, presumably from a minor ampullate gland, and one smaller spigot, presumably from an aciniform gland (figs. 24, 25, 140, 143). The PLS seem to be devoid of functional spigots (figs. 26, 141, 144).

THE FAMILY CAPONIIDAE

Caponiids have a highly modified spinneret arrangement, with the PMS advanced anteriorly and situated between the ALS (figs. 145, 150). In the American species *Nops ovalis* Banks, the ALS of females bears a single major ampullate gland spigot with a fluted base and thin shaft (fig. 146); the piriform gland spigots have stronger shafts and can vary in number even between the right and left spinneret of an individual spider (figs. 145–147). In males, only the major ampullate gland spigot remains (fig. 151); the piriform gland spigots seem to have been lost. It is curious that a loss of piriform gland spigots also occurs (in both sexes) in the gnaphosoid family Ammoxenidae, which resemble caponiids in the anteriorly advanced PMS placement (Platnick, 1990).

The PMS and PLS of both sexes each bear several small spigots equipped with extremely long shafts and presumably serving the aciniform glands (figs. 148, 149, 152, 153). In females, the PMS also bears a single wide spigot (fig. 148) which is absent in males (fig. 152). Because this widened spigot does not occur on the PLS as well, it seems not to be a cylindrical gland spigot, and we hypothesize

that males have lost their minor ampullate glands as well as their piriform glands.

THE FAMILY OCHYROCERATIDAE

In an undescribed species of *Ochyrocera* from Colombia (figs. 162–167), the ALS have a single major ampullate gland spigot, with a long shaft, accompanied by a nubbin that presumably represents a second major ampullate gland spigot (figs. 162, 165). The relatively few piriform gland spigots have short, small shafts. The tetrahedral PMS in both sexes bear only a single spigot (figs. 163, 166); because it is different in shape from the numerous PLS spigots, it probably serves the minor ampullate glands, and the PMS aciniform gland spigots have presumably been lost. The PLS have a single row of aciniform gland spigots, each triangular in outline and flattened, allowing them to be closely packed (figs. 164, 167). A similar arrangement of PLS aciniform gland spigots occurs in the Telemidae and Leptonetidae. Spigots of at least some members of those families also resemble those of *Ochyrocera* in having a highly ridged cuticle, but as this feature occurs in very disparate taxa (including at least some Gradungulidae, Austrochilidae, Segestriidae, Orsolobidae, Archaeidae, and the haplogyne uloborid genus *Waitkera*), its homology is dubious and more detailed studies of the patterns of cuticular and spigot ridging (with scans of greater magnification than those presented here) are needed before the resemblances can be accurately coded.

THE SUPERFAMILY DYSDEROIDEA

Four families (the Dysderidae, Segestriidae, Oonopidae, and Orsolobidae) are included (Forster and Platnick, 1985), and will be discussed together. The silk glands of *Dysdera* have been studied by Millot (1931b) and Glatz (1972). Both authors found only three gland types, and, at least in the synanthropic species *Dysdera crocota* C. L. Koch, there are only three spigot types as well (figs. 168–173). The ALS have a single major ampullate gland spigot (figs. 168, 171), as well as a few piriform gland spigots with reduced bases. The PMS (figs. 169, 172) and PLS (figs. 170, 173) of both sexes seem to be provided only with aciniform gland spigots. Glatz (1972) indi-

cated that the ALS of *Dysdera* are secondarily three-segmented; we have not been able to confirm this (even though the ALS of *Segestria*, for example, are clearly three-segmented), and even Glatz's illustrations (1972: fig. 22A–D) are unconvincing.

The silk glands of *Segestria* were examined by Apstein (1889), Millot (1931b), and Glatz (1972). Apstein reported one (major) ampullate and ten piriform glands serving the ALS, one (minor) ampullate and two aciniform glands serving the PMS, and six aciniform glands serving the PLS. The later workers found minor variation in the numbers of piriform and aciniform glands, but agreed that only four gland types are present. In *Segestria senoculata* (Linnaeus), the ALS (figs. 174, 177) bear a single major ampullate gland spigot with a wider shaft than those of the piriform gland spigots, which have more pronounced bases than in *Dysdera*. In both sexes, the PMS (figs. 175, 178) have one large minor ampullate gland spigot and two smaller aciniform gland spigots, and the PLS (figs. 176, 179) have aciniform gland spigots only, each with ridged cuticle.

Females of two other segestriid genera, *Ariadna* (figs. 154–158) and *Gippsicola* (figs. 159–161) have also been scanned. As in *Segestria*, there is a single, wide major ampullate gland spigot on the ALS (figs. 154, 155, 159). The PMS have one large minor ampullate gland spigot (figs. 156, 160) and one to several aciniform gland spigots. In both genera, some of the PLS aciniform gland spigots are notably enlarged and curved (figs. 157, 158, 161).

In the Oonopidae, we have scanned both sexes of *Dysderina plena* O. P.-Cambridge (figs. 180–185) and unidentified females of *Xyphinus* (figs. 186–190) and *Gamasomorpha* (figs. 191–194) from Singapore. The ALS have one major ampullate gland spigot and only a few piriform gland spigots, originating from low bases (figs. 180, 183, 186–188, 191). The PMS appear to have one minor ampullate gland spigot, with a base higher than those of the aciniform gland spigots (figs. 181, 184, 189, 192, 193). The PLS aciniform gland spigots appear to vary in shaft length (figs. 182, 185, 190, 194).

Among the Orsolobidae, we have scanned both sexes of *Mallecolobus sanus* Forster and

Platnick (figs. 198–203) and females of *Wiltonia graminicola* Forster and Platnick (figs. 204–208), *Maoriata magna* (Forster) (figs. 209–211), and *Subantarctia trina* Forster and Platnick (figs. 212–215). The ALS have a single, relatively large major ampullate gland spigot and piriform gland spigots notable for the almost total lack of bases (figs. 198, 201, 204, 207, 209, 210, 212, 213). The PMS may have one or two minor ampullate gland spigots as well as aciniform gland spigots with longer shafts (figs. 199, 202, 205, 214). The PLS appear to have aciniform gland spigots only (figs. 200, 203, 206, 208, 211, 215).

THE FAMILIES LEPTONETIDAE AND TELEMIDAE

These two families of small, litter- and cave-dwelling spiders have long been of uncertain relationships, for they do not have the chel-iceral lamina of scytodoids or the tracheal and female genitalic modifications of dys-deroids, and thus stand apart from the other taxa classically placed in the Haplogynae. Not surprisingly, the spinnerets of *Appaleptoneta gertschi* (Barrows) (figs. 216–221) and *Usofila pacifica* (Banks) (figs. 222–227) are also strikingly different from those of other haplo-gynes, particularly with regard to their sexual dimorphism.

The ALS are not highly modified, bearing a single major ampullate gland spigot that, especially in *U. pacifica*, is much longer than the piriform gland spigots (figs. 216, 219, 222, 225). The ALS of *A. gertschi* do appear to differ from those of all other classical hap-logyne taxa examined in having distinct, pus-tulose tartipores (fig. 216). The PMS and PLS are strikingly modified in both genera.

In *A. gertschi*, the PMS bear a longitudinal series of closely packed spigots that resemble those forming a similar longitudinal row on the PLS (figs. 217, 220); both series presum-ably serve the aciniform glands. In addition, each PMS bears, along the inner edge of the longitudinal row, two distinct nubbins an-teriorly (in both sexes, figs. 218, 221) and, in females only, one thick-shafted spigot situ-ated more posteriorly (compare figs. 217, 220). A single, similar spigot also occurs, again in females only, along the inner edge of the longitudinal row of PLS aciniform gland spig-ots.

In *U. pacifica*, only the PLS have a row of closely packed aciniform gland spigots (figs. 224, 227). The PMS are tetrahedral; those of males bear only two aciniform gland spigots, with relatively long shafts (fig. 226); those of females have in addition a third spigot, with a short thick shaft. Two similar spigots occur alongside the row of PLS aciniform gland spigots, again in females only (compare figs. 224, 227).

What glands do the spigots restricted to females serve? One could conceivably argue that they serve minor ampullate glands, with the leptonetids and telemids thus joining the eresids and gnaphosoids as taxa with minor ampullate glands serving both the PMS and PLS. This would require an additional hy-pothesis of loss of the minor ampullate glands serving both spinneret pairs in males. It also leaves unexplained the anterior nubbins found on the PMS of both sexes in *A. gertschi* (figs. 218, 221), which at least in terms of their position might best be regarded as remnants of former minor ampullate gland spigots.

The alternative hypothesis, of course, is that the apparently homologous PMS and PLS spigots that appear in females only serve cy-lindrical glands instead, implying that lep-tonetids and telemids might be more closely related to entelegynes than to the other hap-logynes.

No histological work appears to have been done on leptonetids, but the silk glands of the European troglobitic species *Telema tenella* have been investigated by Kovoor and Lopez (1983). Those authors reported four gland types, including the normal ampullate and piriform glands serving the ALS and two types of aciniform glands. Of the latter, type 1 acin-iform glands were found in both sexes, but the type 2 glands occur only in females. Al-though Kovoor and Lopez (1983: 423) did not specifically homologize the type 2 glands with the cylindrical glands of other spiders, they did note that "L'absence du type 2 chez les mâles suggère que la soie de ces glandes aciniformes est utilisée par les femelles pour la confection des cocons ovigères; le manque de glandes tubuliformes conduit également à cette interprétation."

Kovoor (1987), in her subsequent review paper, did not include the Telemidae in her listing of spider families that lack cylindrical

glands, and she does now consider their type 2 glands to be homologous to the cylindrical glands of other spiders (Kovoor, in litt.). In the data matrix below, we have therefore coded cylindrical glands as present in both *A. gertschi* and *U. pacifica*.

THE SUPERFAMILY PALPIMANOIDEA

In the Malagasy archaeid species *Archaea workmani* (O. P.-Cambridge), the ALS have a rotund major ampullate gland spigot accompanied by a nubbin and well separated from the piriform gland spigots (figs. 228, 231). The PMS of males each have two spigots (fig. 232); the smaller, lateral spigot resembles the five spigots found in a single line on the PLS (fig. 233), which all presumably serve the aciniform gland. The larger, medial spigot probably serves a minor ampullate gland. Females have both PMS spigots, the five PLS aciniform gland spigots, and, in addition, two large spigots on the PMS (fig. 229) and three on the PLS (fig. 230) that apparently serve the cylindrical glands.

In the austral family Mecysmaucheniidae, as in several other palpimanoid groups, spinneret and spigot reduction is evident. We have scanned both sexes of the Chilean species *Mecysmauchenius segmentatus* Simon (figs. 234–239) as well as females of *Aotearoa magna* (Forster) from New Zealand (figs. 195–197). The ALS appear to have several piriform gland spigots as well as a nubbin accompanying the major ampullate gland spigot (figs. 195, 196, 237; it is possible that the female *M. segmentatus*, fig. 234, has two functional major ampullate gland spigots). The PMS of females bear a single spigot (fig. 235) similar to the two or three found on the PLS (figs. 197, 236); in *M. segmentatus*, especially, the PMS and PLS are reduced to low mounds bearing the spigots. Males of both genera show no trace of spigots, and the PMS and PLS themselves are almost obsolete (figs. 238, 239). Because no informative comparisons with males are possible, it is difficult to assess what gland types the female PMS and PLS spigots might serve.

The tiny Chilean micropholcommatid *Tricellina gertschi* (Forster and Platnick) (figs. 240–244) also shows relatively few spigots. The ALS have a single major ampullate gland spigot and only three piriform gland spigots (figs. 240, 243). The PMS of males have only one spigot (fig. 244), but females have a second spigot similar in shape to an immediately adjacent, basal spigot on the PLS which is also absent in males (figs. 241, 242). Those adjacent spigots apparently serve cylindrical glands.

The family Huttoniidae, containing the single genus *Huttonia* (endemic to New Zealand), is remarkable for the basally fused PMS (figs. 247, 305) found in both sexes; fused PMS are found elsewhere, to our knowledge, only in some species of the liphistiid genus *Heptathela*. In *Huttonia palpimanoides* O. P.-Cambridge, the ALS have a single large major ampullate gland spigot, apparently not accompanied by a nubbin (figs. 246, 306, 307), although numerous tartipores are present. The PMS of females have numerous aciniform gland spigots with long shafts, a large spigot anteriorly, and two small spigots (one situated posteriorly, and one situated laterally; fig. 247). Probably the anterior spigots serves the minor ampullate glands, and the two smaller spigots the cylindrical glands (as they appear to be absent in males, figs. 308, 309). The PLS appear to have only aciniform gland spigots (figs. 248, 310; the larger spigot in the upper left corner of the micrograph is a PMS spigot).

As noted by Machado (1944: figs. 13, 14), the Palpimanidae are characterized by degenerate PMS and PLS. Our scans of an American representative, *Otiothops pentucus* Chickering (figs. 245, 257–259), agree well with Machado's observation on the Mediterranean species *Palpimanus gibbulus* Dufour. In both genera, the ALS are notable mainly for the nearly linear arrangement of the piriform gland spigots (figs. 245, 258). In females, there is no longer any trace of the PMS or PLS spinnerets; rather, the spigots originate directly from the cuticle (fig. 257) and it is not possible to determine where the division lies between those spigots originally associated with the PMS and those on the PLS. In males, even the spigots have disappeared (fig. 259). As in the mecysmaucheniids, the resulting inability to compare spigot morphology between males and females makes it difficult to identify what glands the spigots remaining in females might serve.

THE FAMILY ULOBORIDAE

The haplogyne New Zealand uloborid *Waitkera waitakerensis* (Chamberlain) resembles other uloborids in spinneret morphology (figs. 260–269; see also Coddington, 1989; Kovoor, 1977b, 1978; Kovoor and Peters, 1988; Peters, 1983; Peters and Kovoor, 1980). The ALS have a large major ampullate gland spigot, with a round base (figs. 262, 268), accompanied by a vestigial nubbin that is more pronounced in females (figs. 260–262) than in males (figs. 266, 268). The piriform gland spigots form an arc extending posteriorly and medially to the major ampullate gland spigot and nubbin.

The PMS are directed laterally, with a conspicuous anterior brush of paracribellar spigots in females (fig. 263) but apparently not in males (fig. 267). Females also have a large PMS spigot, with a greatly widened base (fig. 263), that is presumably a minor ampullate gland spigot (cf. Coddington, 1989: fig. 8), as well as two or three cylindrical gland spigots that are similar to the numerous aciniform gland spigots in base shape but have thicker shafts (fig. 263, with the cylindrical gland spigots immediately anterior to the minor ampullate gland spigots). Males have only a single minor ampullate gland spigot and several aciniform gland spigots (fig. 267).

The PLS of females have a conspicuous, wide pseudoflagelliform gland spigot near the anterolateral margin of the spinning field (figs. 264, 265) as well as about five basally situated cylindrical gland spigots with shorter, wider shafts than those of the numerous aciniform gland spigots. Males apparently lack cylindrical and pseudoflagelliform gland spigots (fig. 269), in the latter case presumably because adult males no longer spin webs utilizing the sticky silk produced by the pseudoflagelliform glands.

THE FAMILY TETRAGNATHIDAE

We present scans for *Tetragnatha versicolor* Walckenaer (figs. 270–275, 282, 287–290) and *Pachygnatha autumnalis* Keyserling (figs. 276–281, 283–286) that complement those of *Leucauge venusta* (Walckenaer) published by Coddington (1989: figs. 22–25) and the histological studies of Apstein (1889) and Sekiguchi (1952).

The ALS major ampullate gland spigot is accompanied in both genera and sexes by a triangular nubbin (figs. 270, 273, 276, 277, 282–284, 288, 289). The PMS of male *T. versicolor* have three small aciniform gland spigots anteriorly, followed by a large minor ampullate gland spigot and what appear to be vestigial remnants of two other such spigots (fig. 274). Females also seem to have the remnants but have in addition an anteriormost cylindrical gland spigot (figs. 271, 290). In *P. autumnalis* males, there are only two aciniform gland spigots plus the functional and vestigial minor ampullate gland spigots (fig. 285), but females have an additional cylindrical gland spigot and appear to lack the vestigial remnant (figs. 278, 279). Females of *L. venusta* do have the remnant (Coddington, 1989: fig. 24).

The PLS of *T. versicolor* show the typical araneoid pattern. Basally, there are two extremely large cylindrical gland spigots in females (figs. 272, 287) but not males (figs. 275). Females have a triplet of one flagelliform and two aggregate gland spigots, but only remnants remain in males. Since the flagelliform and aggregate glands provide base fibers and viscid glue of the sticky lines used in webs, it is not surprising that they atrophy in adult males, which abandon their webs and search for females. Similarly, *P. autumnalis* adults (of both sexes) no longer spin orb webs, and the triplet of spigots is accordingly not observable in either sex (figs. 279–281, 286), although females have a single tiny nubbin in the appropriate area of the spinneret.

THE FAMILY ANAPIDAE

Scans are provided for both sexes of the Chilean species *Crassanapis chilensis* Platnick and Forster (figs. 291–296) and the New Zealand species *Novanapis spinipes* (Forster) (figs. 249–256). As expected, the major ampullate gland spigot of the ALS is accompanied by a nubbin (figs. 249, 253, 291, 294). The PMS of males have at least one anterior aciniform gland spigot and a large posterior minor ampullate gland spigot accompanied by a vestigial remnant bearing a short lobe on its medial side (figs. 254, 295). Females retain the remnant and add one (*C. chilensis*, fig. 292) or two (*N. spinipes*, figs. 250, 252)

cylindrical gland spigots; those of *N. spinipes* have curiously widened and flattened shafts. The PLS of males appear to bear only aciniform gland spigots (figs. 255, 256, 296); females have in addition a large cylindrical gland spigot (figs. 250, 252, 293) and a somewhat smaller spigot, with a widened shaft, that may represent a second cylindrical gland spigot or some remnant of the araneoid triplet. In at least *C. chilensis*, the absence of part or all of the araneoid triplet, even in females, may indicate that the spiders no longer construct orbwebs; Platnick has collected large samples of Chilean anapids from moss and litter, but has never observed orbwebs there comparable to those spun by anapids in New Caledonia and the Neotropics.

CLADISTIC ANALYSIS

A data matrix (table 2) was assembled for 35 genera with haplogyne female genitalia (the first 35 taxa in table 2) and eight entelegyne genera. The entelegynes were added either because some clades represented in the matrix contain both haplogyne and entelegyne genera or because prior work (Coddington, 1990b) suggested that particular cribellate groups had to be considered in any attempt to infer the phylogeny of the "lower" araneomorphs. We added *Deinopis*, *Araneus*, *Mimetus*, and *Pararchaea* to the matrix to represent entelegyne deinopoids, araneoids, and palpimanoids, respectively, and *Oecobius*, *Stegodyphus*, *Dictyna*, and *Callobius* to complete the representation of relevant cribellate clades. These 43 taxa were scored for 67 characters, with codings as follows:

Character 0: Eyes: 8 (0); 6 or fewer, with anterior median pair lost (1); *Nops* and *Mecysmauchenius* are coded as 0 as other caponiid and mecysmaucheniid genera have eight eyes and that number is presumed to be primitive for those families.

Character 1: Cribellum: present (0); lost (1); *Gradungula* and *Pianoa* are coded as 0 because *Progradungula* and *Macrogradungula* have a cribellum, and that state is therefore presumed to be primitive for the family.

Character 2: Chelicerae: without lamina (0), with lamina (1).

Character 3: Serrula: multiple rows of teeth (0); single row of teeth (1).

Character 4: Median cheliceral concavities: absent (0); present (1).

Character 5: Cheliceral diverticula of midgut: absent (0); present (1). As in other features of internal morphology (characters 6, 7, 9, 10, 14, 15) that have been used in prior discussions of hypochiloid and austrochiloid interrelationships, the distributions reported are those expected from the sampling of araneomorphs done by workers such as Millot, Petrunkevitch, and Marples rather than our own investigations; see Platnick (1977) and Forster et al. (1987) for details and references.

Character 6: Dorsal dilator muscles of pharynx: originate on carapace (0); originate on rostrum (1); the polarity of this character is uncertain (Platnick, 1977; Forster et al., 1987; Coddington, 1990a) but its use here to support the monophyly of Hypochilidae could also be met by referring to the ringed spigot morphology apparently unique to that family.

Character 7: Venom glands: limited to chelicerae (0); extend into carapace (1); not applicable in *Waitkera* as uloborids lack venom glands.

Character 8: Sigilla: at least labial sigilla still present (0); lost (1).

Character 9: Coxal glands: duct highly convoluted (0); duct simple, inverted U-shaped (1).

Character 10: Fifth ventral abdominal endosternite: present (0); lost (1).

Character 11: Tarsal claws of legs I and II: similar in size (0); proclaw greatly enlarged (1).

Character 12: Posterior wall of female bursa: unmodified (0); forming separately opening, translucent, pocketlike posterior receptaculum in female genitalia (1); forming distinct posterior receptaculum (2). This character was considered unordered because no special homology between states 1 and 2 has been demonstrated; the posterior female genitalic elements of archaeids and pholcids are not regarded here as homologous with the austrochilid or dysderoid conditions (1 and 2, respectively), and are not coded because they would each be autapomorphies in this context.

Character 13: Margin of all except first tibial trichobothrial base: entire (0); broadly notched (1); crenulate (2). This character was

TABLE 2
Data Matrix

Character	0	5	10	15	20	25	30	35	40	45	50	55	60	65
Hypochilus	00001	11000	00000	00000	00000	00000	00000	00000	00000	00100	00001	-0000	00000	00
Ectatosticta	00001	11000	00000	00000	00000	00000	00000	00010	00000	00100	00000	-0000	00000	00
Gradungula	00010	00111	11020	00100	00000	00000	00000	00001	00001	00000	0000?	-?000	00000	00
Pianoa	00010	00111	11020	00100	00000	00000	00000	00001	00001	00000	0000?	-?000	00000	00
Hickmania	00010	00111	10110	00100	00000	00000	00020	00001	00001	00000	0000?	-1000	00000	00
Austrochilus	00010	00111	10110	01100	00000	00000	00020	00000	00001	00000	0000?	-1000	00000	00
Thaida	00010	00111	10110	01100	00000	00000	00020	00000	00001	00000	00001	-1000	00000	00
Filistata	00110	00101	10001	12000	00000	00000	10011	10001	00001	10000	00010	-1000	00010	11
Kukulcania	00110	00101	10001	12000	00000	00000	10011	10001	00001	10000	00010	-1000	00010	11
Scytodes	11110	00111	10001	12000	00000	00000	-0141	10101	0000-	-0000	00000	-0010	01010	00
Sicarius	11110	00111	10001	12000	00000	00000	-0141	11101	1000-	-0000	00000	-0000	00010	00
Drymusa	11110	00111	10001	12000	00000	00000	-0131	10101	0000-	-0000	00000	-0010	01010	00
Loxosceles	11110	00111	10001	12000	00000	00000	-0141	11101	1000-	-0000	0000-	-0100	01010	00
Diguetia	11110	00111	10001	12000	00000	10001	-0121	10101	1000-	-0000	00000	-200-	11010	10
Segestrioides	11110	00111	10001	12000	00000	10001	-0121	10101	1000-	-0000	00000	-2001	1101?	00
Plectreurys	01110	00111	10001	12000	00001	10000	-0121	10111	100--	-0000	00000	-210-	1111?	00
Kibramoa	01110	00111	10001	12000	00001	10000	-0121	10111	100--	-0000	00000	-2100	1111?	00
Pholcus	01110	00111	10001	12000	00000	00000	-0141	10101	110--	-0000	00000	-1001	1111?	00
Caraimatta	11110	00111	10001	12010	00000	00000	-0020	10111	100--	-0000	0000-	-1000	00110	00
Nops	01110	00111	10001	12010	00000	00000	-0041	10111	1000-	-0000	00000	-1000	00110	00
Ochyrocera	11110	00111	10001	12000	00000	00000	-0130	10101	1101-	-0000	00000	-1000	01010	00
Segestria	11010	00111	10201	12010	00000	00000	-0040	10011	0000-	-0000	00000	-1000	0001?	00
Dysdera	11010	00111	10201	12010	00000	00000	-0040	10011	1000-	-0000	00000	-0000	01010	00
Mallecolobus	11010	00111	10201	12010	00000	00000	-0040	11011	0000-	-0000	00000	-?000	00010	00
Dysderina	11010	00111	10201	12010	00000	00000	-0040	11111	1000-	-0000	00000	-1000	00010	00
Appaleptoneta	11010	00111	10001	12000	00010	00000	-1140	10101	1001-	-0000	00000	00000	00000	00
Usofila	11010	00111	10001	12000	00010	00000	-1040	10101	1001-	-0000	00000	00000	01010	00
Archaea	01010	00111	10001	12001	11110	00000	-0030	00010	1010-	-0001	10000	01000	00001	10
Mecysmauchenius	01010	00111	10001	12001	111?0	00000	-0130	00110	1010-	-0001	10000	??000	00001	00
Tricellina	01010	00111	10001	12001	11010	00000	-0140	00110	1010-	-0000	00000	00000	00000	10
Huttonia	01010	00111	10001	12001	10010	01000	-0140	00010	1010-	-0000	00000	11000	00001	10
Otiothops	01010	00111	10001	12001	100?0	01000	-0140	00110	1010-	-0000	00000	??000	00001	10
Waitkera	00010	00-11	10001	12000	00010	00010	00130	00010	00-01	00000	01002	21000	00000	?0
Tetragnatha	01010	00111	10001	12000	00010	00110	-0130	00010	10-0-	-0100	00103	01000	0000?	?0
Crassanapis	01010	00111	10001	12000	00010	00110	-0130	00100	1010-	-0000	00103	01000	00000	10
Oecobius	00010	00111	10001	12000	00010	00000	00100	00010	10000	11000	00010	01000	00001	10
Stegodyphus	00010	00111	10001	12000	00010	00000	00100	00010	00-00	11000	00012	01000	00001	10
Deinopis	00010	00111	10001	12000	00010	00010	00100	00010	00-01	01000	01002	21000	00001	10
Dictyna	00010	00111	10001	12000	00010	00000	00140	00010	10101	01010	0000?	21000	00000	?0
Callobius	00010	00111	10001	12000	00010	00000	00120	00010	10101	11010	00002	11000	00001	10
Araneus	01010	00111	10001	12000	00010	00110	-0130	00010	0010-	-1100	00003	01000	00000	10
Mimetus	01010	00111	10001	12001	10010	00000	-0130	00010	0010-	-1100	00000	01000	00000	10
Pararchaea	01010	00111	10001	12001	111?0	00000	-0130	00100	1010-	-1100	0000?	??000	00000	10

considered ordered because there does seem to be a special homology between states 1 and 2; although a transformation series of either 0-1-2 or 0-2-1 is conceivable, we do not hypothesize separate 0-1 and 0-2 transformations, and which of the former two orderings is used has no effect on the putative sister-group relationship between the Austrochilidae and Gradungulidae supported by the character. *Appaleptoneta* is coded as 0 because the narrow slit of leptonetid tibial trichobothrial bases is not regarded as homologous with the broad notch of austrochilids and gradungulids.

Character 14: Intestine: M-shaped in lateral view (0); straight (1).

Character 15: Heart ostia: four pairs (0); three or fewer pairs (1).

Character 16: Posterior respiratory system: pair of normal booklungs (0); pair of booklungs each reduced to two separated lamellae

(1); pair of tracheae or modifications thereof (2). This character was considered unordered because the austrochiline condition is not regarded as a necessary step between typical booklungs and tracheae.

Character 17: Clypeus: normal (0); extended along midline into triangular hood projecting over the chelicerae (1); the more dorsally situated structure found in some Mecysmaucheniidae is not regarded as homologous.

Character 18: Opening(s) of posterior respiratory system: posteriorly situated (0); advanced to position just behind openings of anterior respiratory system (1); the coding of *Caraimatta* as 1 is based on Forster and Platnick (1985: fig. 888).

Character 19: Cheliceral peg teeth: absent (0); present (1).

Character 20: Cheliceral gland mound: absent (0); present (1).

Character 21: Pars cephalica: unelevated (0); entire area elevated (1); the elevated ocular area of tetrablemmids and anapids is not regarded as homologous to the carapace shape of some palpimanoid families.

Character 22: Carapace: normal (0); prolonged around elongate chelicerae (1).

Character 23: Cylindrical gland spigots: absent (0); present (1); coded as unknown in *Mecysmauchenius* and *Otiothops* because the absence of all PMS and PLS spigots in males makes the identification of cylindrical gland spigots in their respective females uncertain; coded as 1 for *Oecobius* because *Uroctea* has several cylindrical glands (Kovoor, 1979) and that state is presumed primitive for the Oecobiidae (even though *Uroctea* is ecribellate).

Character 24: ALS anterior hook: absent (0); present (1).

Character 25: PMS anteromedian thick setae on bases with elevated rims: absent (0); present (1).

Character 26: Metatarsi I and II spatulate setae: absent (0); present (1).

Character 27: PLS aggregate gland spigots in females: absent (0); present (1); coded as 1 for *Crassanapis*, which probably makes no web and has probably lost the aggregate and flagelliform spigots, because aggregate glands are presumed to be present in web-building anapids. This character also functions as a summation of 10 synapomorphies for araneoids provided by Coddington (1990a: 44), and was therefore given an initial weight of 10.

Character 28: A summation of 14 synapomorphies for deinopoids plus araneoids (see Coddington, 1990a: 44); these characters are summed here because the monophyly of orbicularians cannot be seriously tested by the selection of taxa in this cladogram, and the summary character was assigned an initial weight of 14.

Character 29: A summation of 2 synapomorphies for Diguetidae (Platnick, 1989a): diamond-shaped endites and wide, semicircular bursa copulatrix shape, given an initial weight of 2. The flattened, laminate male palp of *Diguetia* and *Segestrioides* may prove to be another diguetid synapomorphy when males of *Pertica* are discovered.

Character 30: Cribellate spigots: strobilate (0); claviform (1); *Gradungula* and *Pianoa* are coded as 0 because the cribellate gradun-

gulids have strobilate cribellar spigots; not applicable in any of the remaining ecribellates.

Character 31: Tibial glands: absent (0); present (1).

Character 32: Posterior spiracles: two (0); one (1); *Filistata* and *Kukulcania* are coded as 0 because some filistatid genera have two spiracles (Forster, in prep.) and that state is presumed primitive for the family.

Character 33: ALS major ampullate gland spigots: several (0); three (1); two (2); one plus nubbin (3); one (4). This character seems to be at least partly ordered, in that the two spigots of taxa showing state 2 can be recognized among the three shown by filistatids, and the nubbin is apparently a vestige of the second spigot. However, it is certainly possible that one of the two spigots of state 2 could be lost directly, without going through state 3, or that a transformation between states 1 and 3 could occur. We treated the character as unordered so that congruence with the rest of the data, rather than an imposed order, could determine the results. *Sicarius* is coded as 4 as our scans suggest that no more than one major ampullate gland spigot is present; *Oecobius* is coded as 0 because *Uroctea* has several major ampullate glands (Kovoor, 1979) and that state is presumed primitive for the Oecobiidae.

Character 34: Chelicerae: free (0); fused at base (1). In *Nops* the fusion is confined to the posterobasal cheliceral margin but still appears to be present.

Character 35: Subtegulum and tegulum: separate (0); fused (1); see the comment under character 39 below, which also applies here. The palpal expansion noted by Brignoli (1976, 1979a, b) in some leptonetids presumably reflects retention of remnants of a distal hematodocha only.

Character 36: Tarsal claws of legs: three (0); two (1); *Dysdera* and *Otiothops* are coded as 0 because confamilial genera retain three claws and that state is presumed primitive for those families.

Character 37: Female palpal claw: present (0); absent (1).

Character 38: Labium: fused to sternum (0); free of sternum (1).

Character 39: Male palpal conductor: present (0); lost (1); although the homology of any of the elements of the complex palps of

some palpimanoids with the conductor of other spiders remains uncertain, they are coded as 0 because the conductor is clearly part of the ground plan of Entelegynae at least; this coding minimizes a priori hypotheses of conductor loss when the evidence of homology is equivocal.

Character 40: ALS segment number: three (0); two (1).

Character 41: Tarsi of legs: entire (0); pseudosegmented (1). The divided tarsi of *Nops* are not regarded as homologous with the ochyroceratid-pholcid condition or as plesiomorphic for caponiids; the distally cracked tarsi of male (but not female) plectreurids are also coded as 0.

Character 42: Tapetum of secondary eyes: Homann's (1971) "primitive" type (0); canoe-shaped (1); not applicable in *Stegodyphus, Deinopis, Waitkera,* and *Tetragnatha,* which lack a tapetum.

Character 43: PLS aciniform gland spigots: dispersed (0); in single, closely packed line (1); not applicable in taxa that have lost their PLS spigots (see character 66).

Character 44: Paracribellar spigots: absent (0); present (1); not applicable in ecribellates.

Character 45: Cribellum: entire (0); divided (1); *Gradungula* and *Pianoa* are coded as 0 because *Progradungula* and *Macrogradungula* have an entire cribellum; not applicable in ecribellates.

Character 46: Fertilization ducts: absent (0); present (1).

Character 47: Paracymbium: absent (0); present (1).

Character 48: Retrolateral tibial apophysis: absent (0); present (1).

Character 49: Lateral labral protuberances: absent (0); present (1).

Character 50: Ring of unsclerotized cuticle near base of leg tarsi: absent (0); present (1).

Character 51: A summation of five synapomorphies for Deinopoidea (Coddington, 1990a: 44), assigned an initial weight of 5.

Character 52: A synapomorphy linking (in this matrix) *Tetragnatha* and *Crassanapis* (see Coddington, 1990a, character 78).

Character 53: Major ampullate gland spigots: segregated from piriform gland spigots (0); dispersed among piriform gland spigots (1).

Character 54: Modified spigots on PLS: absent (0), present (1); pseudoflagelliform (2); flagelliform (3). This coding reflects the hypothesis that the differentiated PLS spigots of *Hypochilus* and some other cribellates (state 1) are precursors of the pseudoflagelliform and flagelliform gland spigots of orbicularians, and the character was therefore considered ordered.

Character 55: Number of cylindrical gland spigots on PMS of females: one (0); two (1); more than two (2); not applicable in taxa lacking cylindrical gland spigots (see character 23). This character was considered unordered, as we have no information requiring state 1 to be a precursor of state 2.

Character 56: Number of minor ampullate gland spigots on PMS of females: none (0); one (1); two (2). This character was considered unordered, as we have no information requiring state 1 to be a precursor of state 2.

Character 57: PLS setal pit: absent (0); present (1).

Character 58: Spicules on median surface of PMS: absent (0); present (1).

Character 59: Shaft of piriform gland spigots: normal (0); broadened (1).

Character 60: PMS distal ring composed of fused spigot bases: absent (0); present (1).

Character 61: PMS shape: rounded or digitiform (0); tetrahedral, with flattened posterolateral surface opposing similarly flattened anteromedian surface of PLS (1).

Character 62: Female PLS spigots: present (0); absent (1).

Character 63: Tartipores: present (0); absent (1); *Hypochilus* and *Ectatosticta* are coded as 0 but their putative tartipores (figs. 11, 12; Forster et al., 1987: figs. 33, 36) may represent a different state than the raised structures found in most entelegynes.

Character 64: Transverse ridges on trichobothrial bases: absent (0); present (1).

Character 65: Tarsal organ: exposed (0); capsulate (1); those taxa with an elongated receptor lobe are coded as 0. *Pholcus*, which has a capsulate tarsal organ, is coded as 0 because other pholcids have an exposed tarsal organ and that state is presumed plesiomorphic for the family.

Character 66: Anteromedian row of modified setae on ALS: absent (0); present (1).

The matrix was analyzed using both Hennig86, version 1.5 (Farris, 1988) and

PAUP, version 3.0 (Swofford, 1990). The "m*, bb*" options of Hennig86 (see Platnick, 1989b, for a discussion of the options available in this program) produced 10 equally parsimonious cladograms, each 184 steps long and with consistency and retention indices of 0.56 and 0.83, respectively (see the discussion below for caveats regarding these indices). The same results were obtained from four other Hennig86 options (t, bb*; h, bb*; h*, bb*; m, bb*); five runs of PAUP (using the closest and simple addition sequences, each holding 1 or 10 partial solutions as the initial estimate was constructed, as well as the random addition sequence with 10 repetitions) produced identical results.

The suite of 10 cladograms was then subjected to successive character weighting, a procedure that re-weights the characters on the basis of their relative agreement with the cladograms obtained (Farris, 1969; Carpenter, 1988). Those characters which agree well with the initial cladograms receive greater weight in the ensuing analysis than those which require more homoplasy. Three rounds of successive weighting, implemented through the "xs w; cc; m*; bb*;" commands of Hennig86, produced a stable solution of six equally parsimonious cladograms, each with a length of 568 steps, a consistency index of 0.82, and a retention index of 0.94.

Four of those cladograms are less well resolved than the other two, which have only one trichotomy, and the latter two are preferred because they provide more readily testable hypotheses for future investigation. In addition, when the character weights are returned to their original values, four of the six cladograms (including three of the less well-resolved ones) require 187 steps (three steps more than the original suite of 10 cladograms), whereas the other two require only one additional step (i.e., 185 steps rather than 184). Only one of the cladograms resulting from successive weighting is among the shortest on both the weighted and raw data as well as among the most resolved. Using criteria of parsimony, relative informativeness of characters, and maximum resolution of taxa, we prefer this solution (fig. 311).

The other equally parsimonious (for the weighted data) and maximally resolved solution differs only in the three-taxon statement comprising component 69, placing *Mimetus* as the sister group of component 58. The arrangement shown in component 69 of figure 311 was preferred by Forster and Platnick (1984), on the basis of a character (greatly reduced leg spination) that was not included in this data matrix because, although clearcut within the palpimanoids, it is difficult to code accurately across a broader range of families. The four less well resolved cladograms lacked components 53 and/or 65.

DISCUSSION

Our preferred cladogram, obtained by successive weighting, was not included among the original suite of 10 solutions obtained from the raw data, a point that may require explanation. Given that spider phylogeny is widely construed to have involved numerous instances of parallel reduction (in such features as the presence of a functional cribellum, number of eyes, etc.), and that such repeated losses seem in general to be of less phylogenetic significance than gains of new and complex features, we favor the weighted data and their implications. Our preference, in this regard, is not based on an a priori decision that certain characters (such as cribellum or eye loss) must be less informative than others, but simply on the a posteriori observation that those characters do not agree well with the preponderance of the evidence. In that regard, we note that some authors advocate successive weighting only as a means for selecting among equally parsimonious cladograms. But if the rationale for that usage is that the initial set of cladograms provides us with some information about the relative informativeness of characters, then that must also be the case even when (as we presume will occur with some data sets) there is only a single most parsimonious cladogram produced in an initial analysis, but successive weighting of the data produces multiple solutions.

For those who might favor the raw data instead, we can report that one of the original (and one step shorter) cladograms differs from our preferred solution only in its resolution of relationships within the Dysderoidea. That cladogram shows Orsolobidae (*Mallecolobus*) and Segestriidae (*Segestria*) as sister taxa, with Dysderidae (*Dysdera*) more closely re-

TABLE 3
Behavior of Characters on Figure 311
(In placing steps on the cladogram (last column), three-letter abbreviations refer to terminal taxa, R indicates a reversal, numbers in parentheses refer to character states, tR indicates reversals in terminal taxa, and mult. opt. poss. indicates that different parsimonious optimizations are possible.)

Character	Steps	Consistency	Retention	Weight	Components with steps
0	3	0.33	0.84	2	62, 61, 44
1	3	0.33	0.85	2	72, 69, 57
2	3	0.33	0.84	2	77, 55R, 48R
3	1	1.00	1.00	10	81
4	1	1.00	1.00	10	82
5	1	1.00	1.00	10	82
6	1	1.00	1.00	10	82
7	1	1.00	1.00	10	81
8	2	0.50	0.66	3	81, 71R
9	1	1.00	1.00	10	81
10	1	1.00	1.00	10	81
11	1	1.00	1.00	10	75
12	2	1.00	1.00	10	76(1), 55(2)
13	2	1.00	1.00	10	79(1), 75(2)
14	1	1.00	1.00	10	80
15	1	1.00	1.00	10	80
16	2	1.00	1.00	10	70(1), 80(2)
17	1	1.00	1.00	10	79
18	1	1.00	1.00	10	67
19	1	1.00	1.00	10	69
20	1	1.00	1.00	10	69
21	1	1.00	1.00	10	58
22	1	1.00	1.00	10	51
23	2	0.50	0.92	4	78, 48
24	1	1.00	1.00	10	45
25	1	1.00	1.00	10	52
26	1	1.00	1.00	10	59
27	1	1.00	1.00	10	57
28	1	1.00	1.00	10	63
29	1	1.00	1.00	10	44
30	1	1.00	1.00	10	71
31	1	1.00	1.00	10	48
32	4	0.25	0.81	2	78, 66, 2tR
33	13	0.30	0.62	1	mult. opt. poss.
34	3	0.33	0.81	2	77, 62R, 54R
35	1	1.00	1.00	10	77
36	2	0.50	0.66	3	49, 47
37	8	0.12	0.61	0	mult. opt. poss.
38	6	0.16	0.75	1	78, 62, 45, Ect, 2tR
39	3	0.33	0.89	2	mult. opt. poss.
40	8	0.12	0.58	0	67, 65, 64, 50, 46R, Oec, 2tR
41	2	0.50	0.00	0	Pho, Och
42	1	1.00	1.00	10	73
43	1	1.00	1.00	10	54
44	2	0.50	0.66	3	81, 74R
45	3	0.33	0.50	1	mult. opt. poss.
46	5	0.20	0.42	0	78, 65R, 50R, Par, 1tR
47	5	0.20	0.20	0	mult. opt. poss.
48	1	1.00	1.00	10	64
49	1	1.00	1.00	10	43

TABLE 3—(Continued)

50	1	1.00	1.00	10	43
51	1	1.00	1.00	10	56
52	1	1.00	1.00	10	50
53	2	0.50	0.66	3	74, 71
54	7	0.42	0.75	3	mult. opt. poss.
55	4	0.50	0.33	1	mult. opt. poss.
56	6	0.33	0.66	2	mult. opt. poss.
57	2	0.50	0.50	2	45, Lox
58	1	1.00	1.00	10	46
59	2	0.50	0.00	0	mult. opt. poss.
60	1	1.00	1.00	10	60
61	3	0.33	0.77	2	66, 2tR
62	3	0.33	0.33	1	mult. opt. poss.
63	2	0.50	0.94	4	77, 1tR
64	5	0.20	0.42	0	74, 59, 43, Cal, Dei
65	4	0.25	0.78	2	mult. opt. poss.
66	1	1.00	1.00	10	71

lated to them than to Oonopidae (*Dysderina*). The strict consensus of the 10 original cladograms differs from figure 311 only in duplicating that dysderoid arrangement and lacking components 51, 53, 58, 64, 68, and 73. With the reweighted characters applied, the original 10 cladograms range in length from 571 to 591 steps. Two of them, at 571 steps, are at least nine steps shorter than the others: the one showing the differently (and fully) resolved dysderoid arrangement, and one differing from figure 311 only in that dysderoid arrangement and in lacking component 53. Although familial relationships within the Dysderoidea (and the monophyly of the Oonopidae) remain uncertain, there are at least two characters not included in the matrix (tarsal proprioreceptor bristles and bipectinate tarsal claws) which suggest that orsolobids are more closely related to oonopids than to segestriids (Forster and Platnick, 1985), and that the successively weighted dysderoid resolution is therefore preferable.

In our initial coding, four characters (27–29 and 51) were given extra weight to represent suites of synapomorphies suggested by prior work on Diguetidae, Orbiculariae, Deinopoidea, and Araneoidea. It is unlikely that all of these 31 implied synapomorphies would be free of homoplasy if actually scored for all the taxa considered here (even though the groups they imply would almost certainly remain monophyletic); many are behavioral traits that would lead to large numbers of missing entries if so coded. The consistency and retention indices reported here are therefore only approximations. If these weights are reset to 1, the initial 10 cladograms obtained have a length of 157 and a consistency index of 0.43, a figure that better represents the fit of the data in table 2 to figure 311. However, the initial weights apparently had relatively little effect on the results. If one initially weights character 28 (14 putative orbicularian synapomorphies) as 2, and all other characters as 1, 14 cladograms are found (with a length of 158 steps, a consistency index of 0.49, and a retention index of 0.80), and successive weighting on those produces four cladograms, including the one preferred here.

For the preferred solution, the behavior of the characters is shown in table 3; for each character, we list (1) the number of steps, (2) the consistency index, (3) the retention index, (4) the weight received in the final two rounds of successive weighting, and (5) the components where steps occur (when there is no ambiguity in optimization). All but two of the components are supported by at least one unambiguous step change. Component 68 is supported by a change required in character 54 under any optimization (and possibly by changes in characters 33, 45, and 55, under some optimizations). Component 53 is supported by possible changes in characters 45 and 56.
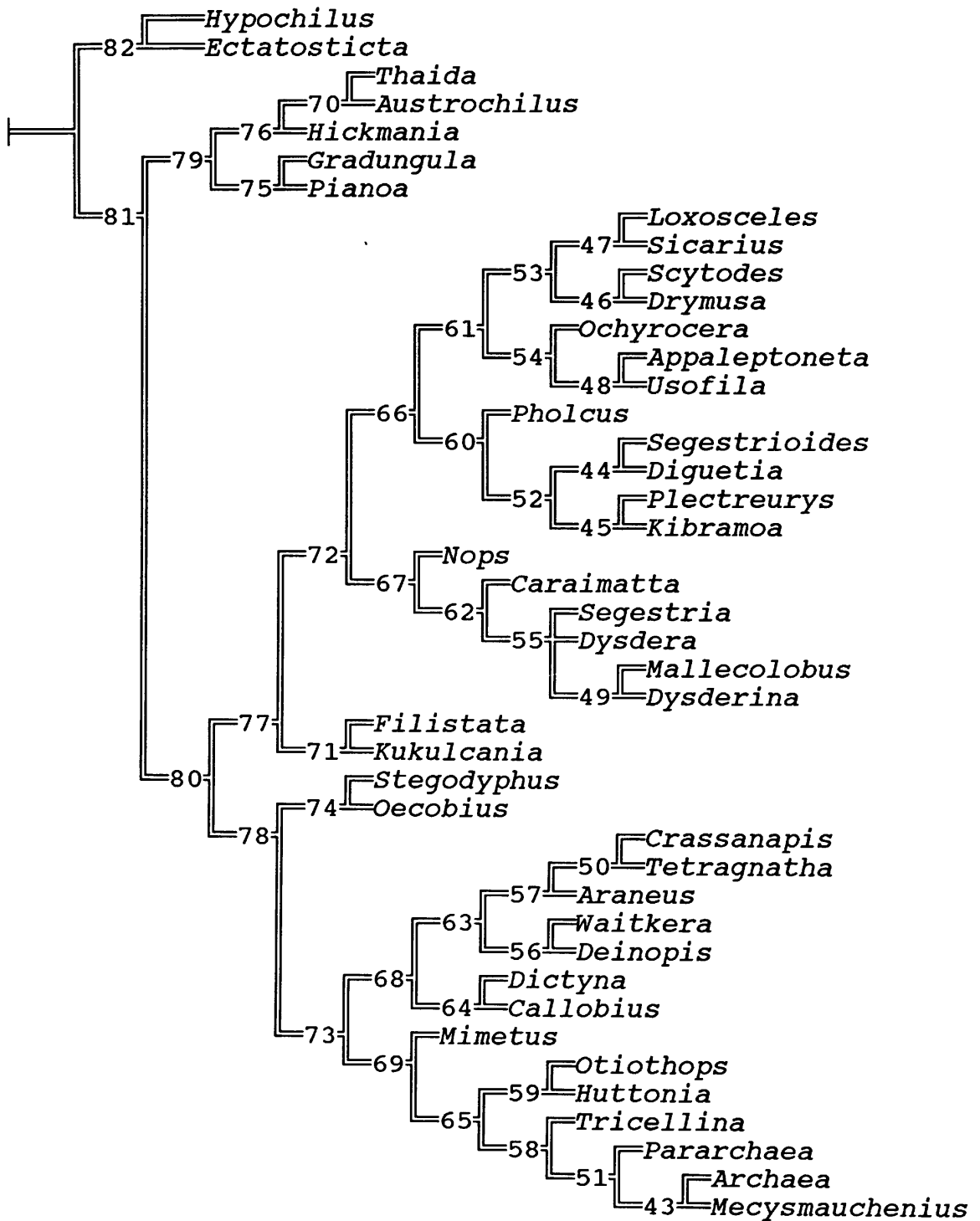
Fig. 311. Preferred cladogram for the 43 taxa listed in table 2. The two hypochilid genera have been united on the basis of comparisons with liphistiids and mygalomorphs not included in the matrix (Forster et al., 1987). See text for commentary.

CONCLUSIONS

Our preferred cladogram (fig. 311) reflects several groups proposed and justified previously: i.e., the Palaeocribellatae (node 82), Neocribellatae (node 81), and Austrochiloidea (node 79) (Forster et al., 1987); the Araneoclada (node 80: Platnick, 1977); Palpimanoidea (node 69: Forster and Platnick, 1984); Dysderoidea (node 55: Forster and Platnick, 1985); Telemidae plus Leptonetidae (node 48: Platnick, 1986); Diguetidae (node 44: Platnick, 1989a); and Orbiculariae (node 63: Coddington, 1990a, 1990b). The cited publications proposed ingroup structures for the Austrochiloidea, Orbiculariae, and Palpimanoidea, and require no further discussion (although we note that a reduction to two major ampullate gland spigots is new evidence supporting the relimitation of Austrochilidae proposed by Forster et al., 1987).

Our cladogram also includes several groupings never before proposed or explicitly justified. A number of the characters introduced in this study, particularly spinneret characters, have proven phylogenetically informative. To justify the new groups proposed, and to underscore the informativeness of several new characters, we discuss below the character support for many of the nodes on this cladogram. Not all possible character changes are noted; only those at each node with the highest consistencies are reported. The genera on the cladogram are discussed as exemplars of the higher taxa to which they belong.

The classical Haplogynae emerges as monophyletic, supported at node 77 by the origin of the cheliceral lamina (character 2; subsequently lost at nodes 48 and 55), basal fusion of the chelicerae (character 34; subsequently reversed at nodes 54 and 62), fusion of the tegulum and subtegulum (character 35), and the loss of tartipores (character 63, with their reappearance in *Appaleptoneta*). Its sister group is the Entelegynae, supported at node 78 by the origin of cylindrical gland spigots (character 23; with an apparent parallelism at node 48 for *Appaleptoneta* plus *Usofila*), separation of the labium and sternum (character 38; subsequently reversed in *Crassanapis* and *Pararchea*), and the development of fertilization ducts (character 46).

Additional evidence for the monophyly of the Entelegynae comes from Eberhard (1988), who suggested that cribellate silk-combing behavior, in which both legs IV are braced against each other and move simultaneously, is a derived character uniting at least the oecobiids, eresids, amaurobiids, dictynids, deinopids, and uloborids. Secondary haplogyny (loss of fertilization ducts) is required at least twice in the Orbiculariae (for *Waitkera*, and at node 50 for *Crassanapis* plus *Tetragnatha*) and at least once in the Palpimanoidea at node 65. Optimization of character 46 on this tree requires a parallel appearance of fertilization ducts in *Pararchea*: this outcome is a result of the choice of the haplogyne *Tricellina* to represent the Micropholcommatidae. However, other micropholcommatids are entelegyne, and future work may show that secondary haplogyny has appeared in parallel at nodes 59 and 43. Note that without more knowledge of the cladistic structure within each of the four possible cases of secondarily haplogyne genitalia (Uloboridae, Tetragnathidae, Anapidae, Palpimanoidea), we cannot rule out the inference of secondarily entelegyne genitalia as well. That is, although these data support the inference of the loss of the entelegyne condition in each case, they do not exclude the possibility that these instances of secondarily haplogyne genitalia subsequently gave rise to the entelegyne condition in some or all of the entelegyne members of each clade. In fact, the cladistic analysis of uloborid genera presented by Coddington (1990a) implies secondarily entelegyne genitalia in the genus *Polenecia*.

Within the Entelegynae, *Dictyna* and *Callobius* are united at node 64 by the origin of the retrolateral tibial apophysis on the male palp (character 48), the Orbiculariae and *Dictyna* plus *Callobius* are united at node 68 by modification of apical spigots on the PLS into pseudoflagelliform spigots (character 54, state 2), and this group is united with the Palpimanoidea at node 73 by the origin of the canoe-shaped tapetum (character 42). *Stegodyphus* and *Oecobius* are newly united at node 74 by the loss of the PMS paracribellum (character 44) and dispersal of the major ampullate gland spigots in the piriform field (character 53, with a parallelism in the filistatids). In the analysis of Coddington (1990b),

Oecobiidae and Eresidae emerged as successive outgroups to the rest of the Entelegynae. The rearrangment proposed here results mainly from recognizing the filistatid PMS specialized spigots as paracribellar homologs. Coddington (1990b) mentioned this possibility, but elected to code the paracribellum in Filistatidae as absent, pending additional comparative data. On that cladogram, therefore, it appeared once in Austrochilidae and once within the clade distal to Oecobiidae and Eresidae. Under the new coding, the paracribellum evolved once at Neocribellatae (node 81) but was lost in Oecobiidae and Eresidae.

Within the classic Haplogynae, *Caraimatta* is united with the Dysderoidea at node 62 by the loss of the anterior median eyes (character 0) and loss of the basal fusion of the chelicerae (character 34), and these are united with *Nops* at node 67 by having the openings of the posterior respiratory system advanced to just behind the openings of the anterior respiratory system (character 18). *Loxosceles* and *Sicarius* are united at node 47 by loss of the inferior tarsal claw (character 36), and the unique spicules on the median surface of the PMS (character 58) unite *Scytodes* and *Drymusa* at node 46. Evidence supporting node 53 is thin, but one possible optimization of character 56 (loss of minor ampullate glands on the PMS of females) supports this node; parallel loss of the minor ampullate gland spigots is then required at node 48. *Ochyrocera* is united with *Appaleptoneta* plus *Usofila* at node 54 by a loss of the basal cheliceral fusion (character 34) and by the unique linear arrangement of the PLS aciniform gland spigots (character 43), and these are united with the sicariids, drymusids, and scytodids at node 61 by loss of the AME (character 0). The ALS anterior hook (character 24), separate labium (character 38), and deep PLS setal pit (character 57; a shallower pit occurs in *Loxosceles*) characterize the Plectreuridae (node 45). Plectreurids and diguetids are united at node 52 by the unique PMS anteromedian thick setae arising from bases with thick rims (character 25), and at node 60 these families are united with *Pholcus* by the unique PMS distal ring composed of fused spigot bases (character 60). Piriform gland spigots with broad, flattened shafts (character 59) may also unite the pholcids, plectreurids, and diguetids: one optimization of this character suggests its origin at node 60 with subsequent reversal to round shafts in *Kibramoa* (states in *Diguetia* and *Plectreurys* are unknown as they have lost their piriform spigots). Reduction of posterior spiracles to one (character 32) and tetrahedral PMS (character 61) support node 66; reversals are required for each character in some terminal taxa. The peculiar filistatids (node 71) share the unique claviform cribellate spigots (character 30) and anteromedian row of modified setae on the ALS (character 66); their sister group comprises several classic haplogyne families united at node 72 by loss of the cribellum (character 1).

To our surprise, the classical Scytodoidea did not emerge as monophyletic on this cladogram, which treats the cheliceral lamina (character 2) as a synapomorphy of Haplogynae that was lost independently in the Dysderoidea and in the leptonetid-telemid lineage.

Cylindrical glands emerge as a parallelism, independently acquired by the leptonetid-telemid lineage and the Entelegynae (it is curious, to say the least, that leptonetids also seem to be unique among the classical haplogynes in having tartipores). They may also have appeared independently in the mygalomorph family Atypidae, where Glatz (1973) reported a spigot type, occurring on both the posterior median and posterior lateral spinnerets, unique to adult females; Glatz found no glands serving those spigots and surmised that they had not yet appeared in the ontogeny of the specimens he examined, and that they probably produce silk for use in egg sac construction. In any case, if cylindrical glands are synapomorphic at the level of Entelegynae, the absence of those glands in a few entelegyne groups represents one or more independent losses, and those entelegynes lacking cylindrical glands could be associated on that basis. This might render a clubionoid-salticid association feasible (see also Ono, 1987, for similar considerations; however, as his genus *Humua* seems to be correctly placed as a castianeirine, it probably does have cylindrical glands).

With regard to classification, there is at least one implication of this study worthy of note.

The limits of the family Sicariidae have long been unstable. As recognized by Simon (1893), the family included a variety of taxa now generally placed as independent families (e.g., Plectreuridae, Diguetidae, Loxoscelidae, Scytodidae, and Drymusidae, as well as the enigmatic New Zealand genus *Periegops* Simon). Some recent authors have responded to the relatively small numbers of genera currently assigned to these families by suggesting various familial re-mergers; Brignoli (1980), for example, suggested reuniting the Scytodidae and Sicariidae. Simon's Sicariidae is diphyletic on our cladogram, and authors from F. O. P.-Cambridge (1899) to Gertsch (1949, 1958) thus appear to have been justified in removing diguetids and plectreurids from the group.

A branching diagram for scytodoids was provided by Lehtinen (1986); it is not particularly congruent with ours (which is scarcely surprising, since it includes groupings unsupported by any putative synapomorphies). As only body regions—rather than actual characters—were associated with its branches, we are unable to include Lehtinen's data, whatever they were, in our matrix. Two features were stressed by Lehtinen, however, and deserve further comment. One, his distinction between "unpaired versus paired vulva," is often arbitrary; diguetids, for example, were said to have an unpaired vulva but a median receptaculum is found only in *Diguetia*, and *Segestrioides* even has a pair of lateral poreplates (Platnick, 1989a). Median receptacula associated with the anterior and posterior faces of the bursa cannot be considered homologous to each other. A second feature stressed by Lehtinen, the epiandrous spigots associated with the male gonopore, are potentially very informative, but will require a scanning electron microscopic survey comparable to the one provided here for spinneret spigots before their implications can be assessed.

Despite the diphyly of Simon's Sicariidae, our cladogram suggests that *Sicarius* (the only currently recognized member of the Sicariidae) and *Loxosceles* (the only currently recognized member of the Loxoscelidae) are sister groups. Because of their monogeneric nature, these two family-group names currently perform no useful grouping function,

and we therefore advocate placement of the Loxoscelidae as a junior synonym of the Sicariidae. This new grouping, we note, is useful in that it stresses the putative sister-group relationship between the only two genera considered here which are known to have venom that is extremely dangerous to humans (Newlands, 1984). A similar argument could be advanced regarding the familial status of the Scytodidae and Drymusidae, which are also each currently monogeneric, but we expect additional genera to be described in both families in the near future, and therefore prefer to retain those names.

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